DOCTORAL THESIS

Diet, habitat, use and conservation ecology of the golden-backed uacari, Cacajao melanocephalus ouakary, in Jaù National Park, Amazonian Brazil

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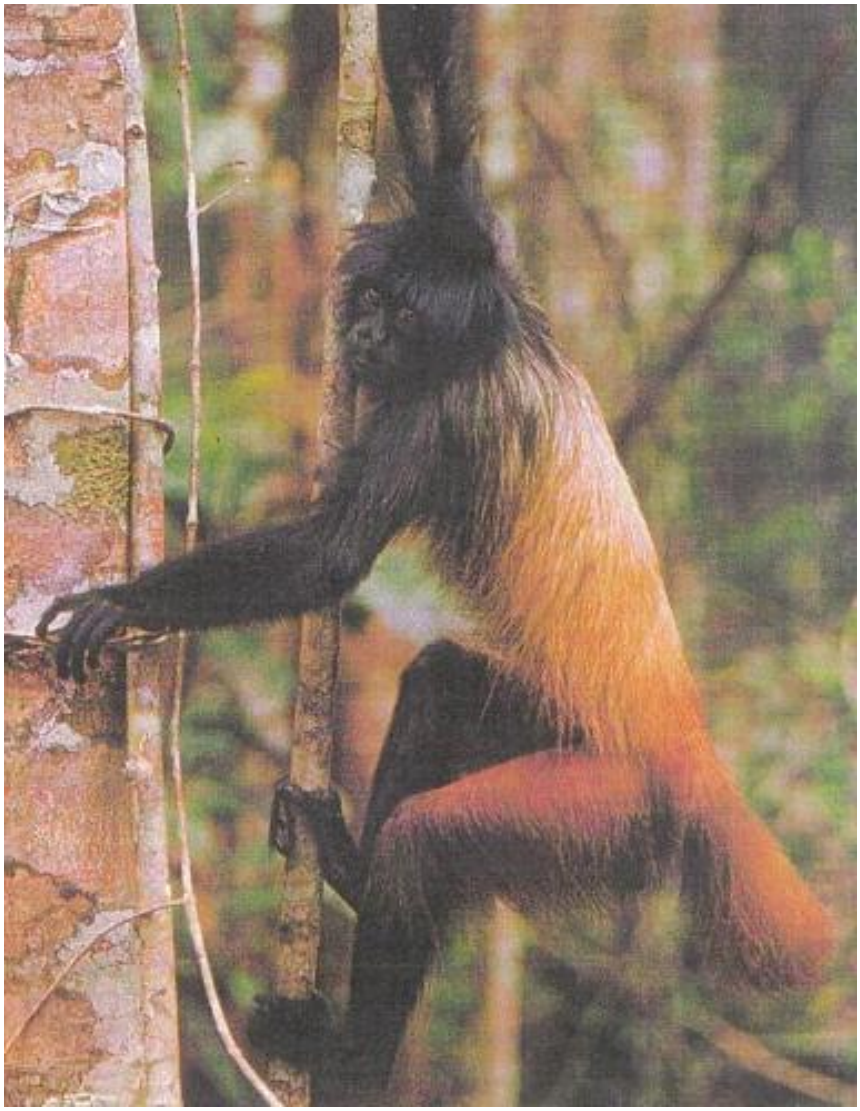
DIET, HABITAT USE AND CONSERVATION ECOLOGY OF THE GOLDEN-BACKED UACARI, *Cacajao melanocephalus ouakary*, IN JAÚ NATIONAL PARK, AMAZONIAN BRAZIL

Adrian A. Barnett



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ABSTRACT

The feeding ecology, general behaviour, size of groups and use of habitat of the golden-backed uacari, *Cacajao melanocephalus ouakary*, was monitored for 14 of a 19-month period in Jaú National Park, Amazonian Brazil between October 2006 and April 2008. The botanical composition and phenology of the habitats was also studied.

The diet is dominated by seeds of immature hard-husked fruits. Leaves, flowers and pith served as fall-back foods. The diet items eaten were the most abundant at the moment, with items previously ignored incorporated when the abundance of other foods dropped relative to them. Most feeding occurred in the forests upper strata, but with occasional visits to the ground and low bushes when little food was available elsewhere. Feeding bouts were short, with uacaris generally spending less than three minutes in a feeding patch before moving to the next. Individual adults generally foraged one-per-patch, though up to five animals might forage simultaneously in canopies of very large trees. Uacaris were recorded feeding on 136 plant species. *Micropholis venulosa, Echweilera tenuifolia*, *Buchenavia ochrograma, Pouteria elegans* and *Mabea nitida* were the most abundant species in the diet, and were eaten for both leaves and seeds. Flowers of *E. tenuifolia* were also eaten. The most important diet families were Sapotaceae, Fabaceae and Lecythidaceae. Invertebrates represented less than 2% of the diet, and were mostly ants, termites and caterpillars. Many were free-ranging, but shoot-boring larvae were also extracted and eaten. Additionally, fruits of five species were recorded being eaten with insect larvae still living inside them.

Uacaris use two habitats, terra firme (a never-flooded mosaic of several forest sub-types) and igapó (a seasonally-flooded forest that occurs between terra firme and the open river). Igapó's fruiting season match the flood pulse and so are strongly condensed. Those of terra firme are less so. In 14 month, uacaris were seen exclusively in terra firme during 3 months, only in igapó during 9 months and in both during 2 months. Movement between the habitats appears to follow fruit availability. When there is little fruit in either, uacaris remain in the igapó and feed (mostly) on new leaves.

The activity budget was dominated by moving, paused feeding and feeding-while-moving. Very little resting was observed and almost no physical social interactions such as aggression or grooming. Adult *C. m. ouakary* were rarely seen closer than 6m apart, and groups were often diffuse, spreading over several hundred meters. Reproduction appears to occur twice a year, very young animals being seen in December and May. Observed group size varied between 2 and 51. Groups of 6-15 were most commonly seen. Group size varied with the season and habitat, being largest (30-51) in never-flooded rainforest and smallest (4-6) in the igapó when little fruit was available and fall-back foods dominated the diet.

At least 10 of the species in the *C. m. ouakary* diet are used as timber in Amazonia. While this is not a cause of conflict in Jaú National Park, it might be so elsewhere in the animal's range. This has been the first long-term study of the ecology of golden-backed uacaris in Brazil and suggestions are made for future research.

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This thesis is dedicated to my parents, Donald Ashton Barnett & Kathleen Mary Barnett, my sister Karen and to my wife, Eliana Barnett-Andrade.

TABLE OF CONTENTS

TABLES

FIGURES		
		Page
I-1	Distribution *Cacajao* taxa and Previous Study Sites	9
I-2	The Skull of *Cacajao m. ouakary*	14
I-3	The Head of *Cacajao m. ouakary*	16
I-4	Igapó Forms a Narrow Band of Flooded Forest	27
I-5	Várzea from the Air, Showing Broad Floodplain	27
II-1	Monthly Variation of Rainfall and Riverwater Levels in Central Amazonia	49
II-2	Map of Jaú National Park, Showing Research Site	50
II-3	Geology of Jaú	55
II-4	Habitats Sampled with Quadrats	56
II-5	Research Site showing Trails, Quadrat Locations and Primate Study Zones	64
II-6	Floating Seeds in Igapó, a Seed Spoon to Access them Without Eye-infections	76
II-7	Examples of Flowers Eaten by *C. m. ouakary*	79
II-8	Species-specific Fruit-damage Patterns	81
II-9	Using Munsell Color Charts to Assess Fruit Colour	84
II-10	Equipment for Quantifying Fruit Penetrability	86
II-11	Insect Bore Holes, Indicating an Infested Seed	90
II-12	Larval Insect Tracks in a Uacari Diet Fruit	92
II-13	Field Guide Roberto with a Canoe used for Surveys and Sample Collecting	94
III-1	Distribution of DBH of Trees, Palms and Lianas by Habitat	111
III-2	Number of Tree Species per Plant Family	112

CHAPTER 1

INTRODUCTION

... les dentes incisives très longues et dirigées comme celles des lapins, c'est a dire, proéminentes et fort avancées.

Johann Baptist von Spix, 1823 (part of original description of the Golden-backed Uacari)

1.1 General Introduction

Until the start of the current study of dietary ecology and a contemporaneous one of social ecology and communication (Bezerra, 2010), the golden-backed uacari, *Cacajao melanocephalus ouakary*, had never been the subject of a long-term study. Its general ecology had been studied in Colombia and a couple of short studies in Brazil had given glimpses of the animal's ecology, but no detailed studies had been done. This study represents an attempt to gain the first ever quantitative data on diet and habitat use in the golden-backed uacari and investigate the bases of its diet and habitat choice.

This chapter covers the current state of our knowledge of golden-backed uacari ecology and social biology. A description of the pertinent aspects of anatomy and morphology is also provided. Because there is very little actual information about *C. m. ouakary*, data from other members of the genus (or family) are provided when there is a gap in the knowledge for *C. m. ouakary*, with the expectation that the situation for this species will be similar enough for such data to provide a useful guideline.

1.2 Taxonomy, Etymology and Evolution

1.2.1 The Broad Picture

Cacajao m. ouakary is a Neotropical monkey belonging to the family Pitheciidae (Groves, 2001), a group that also includes the genera *Pithecia* (sakis), and *Chiropotes* (bearded

sakis). Titi monkeys (genus *Callicebus*) are also included in this group by some authors (e.g. Horovitz *et al*., 1998), as (less frequently) are night monkeys (*Aotus*: e.g. Ford, 1986). Tejedor (1998) reviews the phylogenetic position of *Aotus* and *Callicebus.* The members of the family Pitheciidae recognised by Groves (2001) are given in Table 1-I.

Table I-1: Classification of the Uacaris and their Relatives (after Groves, 2001)

Order: Primates
Sub-order: Haplorrhini
Infraorder: Eusimiiformes
Super-family: Platyrrhini
Family: Pitheciidae
Sub-family: Callicebinae (titi monkeys)
Genus: *Callicebus* (15 species)
Sub-family: Pitheciinae (sakis and uacaris)
Genus: *Pithecia* (sakis, 5 species)
Genus: *Chiropotes* (bearded sakis, 2 species)
Genus: *Cacacjao* (2 species)
Species: *Cacajao calvus* (Bald uacaris)
Sub-species: *C. calvus calvus* (White bald uacari)
C. c. novaesi (Novaes' or Yellow-naped bald uacari)
C. c. rubicundus (Brazilian red uacari)
C. c. ucayalii (Peruvian red uacari)
Species: *Cacajao melanocephalus* (Black-headed uacaris)
Sub-species: *C. m. melanocephalus* (Black-backed uacari)
Sub-species: *C. m. ouakary* (Golden-backed uacari)

1.2.2 The Most Recent Taxonomic Changes

Since Groves (2001) studies were published, there have been a number of taxonomic revisions which, whilst adhering to Groves' taxonomy above the species level, have modified it at the level of species and subspecies. Thus, the treatments of Van Roosmalen *et al.* (2002), Wallace *et al*. (2006), Defler *et al.* (2010) and Ferrari *et al.* (2010) have together raised the number of recognised *Callibecus* species to over 30 (though some of these divisions have been disputed by Defler, 2004). Silva Jr. & Figueredo's (2002) analysis of *Chiropotes* agreed that *Ch. albinasus* was monotypic, but raised the four taxa

Groves (2001) had considered to be sub-species of *Ch. satanus* to the level of species. Consequently, there are now five accepted species of bearded saki (*Ch. albinasus, Ch. chiropotes, Ch. sagulatus, Ch. satanus* and *Ch. utahickae*). Boubli et al. (2008) had renamed the melanocephalus taxon *C. honshomi*, given the name *C. melanocephalus* to the taxon formely known as *ouakary*, and erected a new taxon *C. ayresi* (see Section 1.2.6). However, the most recent taxonomic treatment of the uacaris (Ferrari *et al*., 2010, submitted) lists two species of *Cacajao, C. melanocephalus* and *C. ouakary*: the former with two sub-species (*C. m. melanocephalus* and *C. m. ayresi*), the latter monomorphic. Given this confusion, this thesis follows Hershkovitz (1987) and Groves (2001) and uses *C. m. melanocephalus* for populations north and east of the Rio Negro (black-backed uacaris), and *C. m. ouakary* for south and west of the Rio Negro (golden-backed uacaris). Until the statuses of these taxa are resolved, the status of *C. ayresii* is considered here to be *incertae sedis.*

Note: In her thesis on the vocal behaviour of uacaris, Bezerra (2010) followes the taxonomy of Boubli et al. (2008), using *C. melanocephalus* for the golden-backed uacaris of Jaú.

1.2.3 Pitheciine Relationships

Pithecia, Chiropotes, Cacajao and *Callicebus* have been recognised as a natural group, ever since Mivart's (1865) pioneering reorganization of primate taxonomy and systematics. Once a sub-family of the Cebidae (e.g. Hershkovitz, 1987a), the four genera were elevated to family level by Horovitz *et al.* (1998), and by Groves (2001). Cladistic analysis of the β²-microglobulin gene by Canavez *et al.* (1999) showed that the two pitheciine sub-families (Pitheciinae and Callicebiinae) were each monophyletic clades, and further confirmation has occurred with molecular phylogenies using a variety of

genes, including cytochrome c (Meldrum, 1995), IRBP intron 1 and epsilon-globin sequences (Schneider *et al.,* 1996), epsilon-globin locus and 5' flanking regions (Porter *et al*., 1997), FUT1 nuclear gene (Borges & Harada, 2002), prion protein (Schneider *et al.*, 2004), six nuclear genes (Opazo et al., 2006), and nuclear DNA markers (Wildman *et al*., 2009). Karyotypic analysis (e.g. Dutrilleaux, 1992) also supports this position.

Within the Pithecinae, a number of analyses have concluded that *Pithecia* is the least derived taxon, with *Cacajao* and *Chiropotes* formed a closely-related, but more derived, natural grouping (e.g. Auricchio, 2000; Corruccini, 2001; Dutrillaux, 1992; Figuereiro, 2006; Hugot, 1998; Opazo et al., 2006; Schneider, 2000; Schneider *et al*., 1996). Analysis of mitochondrial DNA by Boubli & Ditchfield (2000) suggests that *Cacajao* and *Chiropotes* diverged from a common ancestral stock in the mid-Miocene, some 9 million years ago (Mya). A LCA (last common ancestor) analysis morlecular nalysis by Opazo et al. (2006) analysis places the divergence at 6.68 Mya. These authors note that this date is close to the boundary (7 million years) generally accepted (see Wildlman & Goodman 2004) as that required to generate differences sufficient to merit generic status. This agrees with the suggestion of Barnett & Brandon-Jones (1997) that *Cacajao* and *Chiropotes* did not warrant full generic rank and that they should be combined. This was followed by Goodman *et al.* (1998), who formally suggested that the two genera be combined, with *Chiropotes* taking priority (because, though both names had been proposed by Lesson (1840) in the same paper, *Chiropotes* came 3 pages before *Cacajao,* and threfore has priority). Commenting on this, Groves (2001) noted ‘a final decision on the acceptability of this proposal must await more complete evidence and a consensus on rank/time association` (Groves, 2001: p. 169). However, Opazo et al. (2006) noted that

though LCA methodology dated to node to 6.68 Mya, the Bayesian method give a date of 7.05-7.8 Mya. More recent authors (e.g. Figuereiro, 2006) have continued to maintain the separateness of two genera. De Miranda Ribeiro (1940) proposed sub-generic distinctions within the genus *Cacajao,* with *Cacajao* (*Neocotharus*) to accommodate black-faced uacaris, and *Cacajao* (*Cacajao*) for red-faced ones. Though useful, this schema has not been widely adopted.

1.2.4 Uacari Etymology

Members of the genus *Cacajao* are commonly known as 'uacaris' (sometimes spelt 'uakaris'). Both the word 'cacajao' and 'uacari' have their origins in indigenous languages (Barnett, 2004). Their original meanings are now lost, as the root languages (for 'cacajao', Baré; and either Tarumã, Mura or Juma, for 'uacari') became extinct before they could be recorded and analysed linguistically (Barnett, 2004).

1.2.5 Uacari Evolution

The genus *Cacajao* comprises two evolutionary lineages, the 'red-faced' and the 'black-faced' clades (Hershkovitz, 1987a; de Figueiredo, 2006). The evolutionary lineages split some 5 million years ago (early Pliocene: Boubli & Ditchfield, 2000). The red-faced clade, characterized by a naked bald head with depigmented facial skin, encompasses four described sub-species of *C. calvus* (*C. c. calvus, C. c. novaesi, C. c. rubicundus* and *C. c. ucayalii*), and a possible undescribed fifth. The black-faced clade, meanwhile, has black hair on the head and pigmented facial skin and consists of three taxa; the *incertae sedis* taxon *ayresii, C. m. melanocephalus* and *C. m. ouakary.* The first two occur north and east of the Rio Negro, the final one to the south and west of it (Fig. I-1). The latter species, commonly known as the golden-backed uacari, is the object of this study.

1.2.6 History of Uacari Discovery and Taxonomy

Cacajao melanocephalus ouakary was originally described as *Brachyurus ouakary* by the German explorer-naturalist Johann von Spix in 1823 from a specimen he collected in February 1820 while visiting the lower Rio Negro as part of his 1819-1820 exploration of the Brazilian Amazon (Fittkau, 2001; Spix & Martius, 1824). The species was long conflated with another uacari, a form described as *Simia melanocephala* by Alexander von Humboldt in 1812. This conflation began with Wagner (1833) who regarded Spix's animal as a juvenile of the species described by Humboldt (though Humboldt's animal is, in fact, a juvenile, while Spix's animal is an adult male). Early primate taxonomists used *'Simia'* in a rather profligate manner, so that by the early 19th Century it contained species from several modern genera, including both Old and New World taxa (Groves, 2008). Various early workers on primate taxonomy such as Erxleben (in 1777), Hofmanseg (in 1807) and E. Geoffroy Saint-Hilaire (in 1812) recognized that the genus no longer represented a natural grouping and began to split it up (Groves, 2001) and '*Simia*' was finally suppressed by the International Commission on Zoological Nomenclature with Opinion 114 in 1929 (Groves, 2008). Thus, Spix, who considered his animal to be a separate species from Humboldt's (Spix & Martius, 1824), did not follow Humboldt's generic terminology, but instead coined the generic name *Brachyurus* (meaning 'short tail'). However, because Humboldt published first, when Wagner conflated the two species, the two were known under the name of *Brachyurus melanocephalus.* The generic name *Brachyurus* was eventually dropped because the name was already in use for a genus of beetle, and the name 'cacajao', proposed by the French taxonomist J.P. Lesson in 1840, then replaced it (Barnett, 2005; Hershkovitz 1987a).

The four geographically separated populations of red-faced uacaris (see above) appear very distinctive, and differ greatly in pelage colour. Though the possibility that each might be a full species has been mooted (Bowler, 2007; Groves, 2001), genetic analysis by de Figueredo (2006), and combined morphometric and generic analysis by de Figueredo & Silva Jr. (in press) has confirmed the opinion of Hershkovitz (1987a) that each represents a sub-species and does not merit elevation to a full species. The status of a fifth taxon, announced by Silva Jr. & Martins (1999) from the Rio Jurupari (an affluent of the Juruá, see Fig. I-1), remains unresolved.

In 1987, as a result of studies of the morphology, anatomy and pelage characteristics of museum specimens, Philip Hershkovitz recognised the two taxa of black-faced uacaris as taxonomically distinct, and proposed the name *C. melanocephalus melanocephalus* for those populations occurring in the forests on and above the north bank of the Rio Negro (that is, the area and uacari populations from which Humboldt collected his specimen), and *C. m. ouakary* for those on the southern side (those areas from which Spix collected his). This elevation followed an earlier (informal) proposal by the Colombian primatologist Jorge Hernandez-Camacho (Hernandez-Camacho & Cooper, 1976). More recently, genetic analyses by Wilsea Figueredo (de Figueredo, 2006) caused her to raise these two sub-species to full species status; *C. melanocephalus* and *C. ouakary*, respectively.

In 2008, Boubli *et al*. published a taxonomic revision of black-faced uacaris. In this they followed de Figueredo (2006) in raising the two existing taxa to species level, while adding a third species, *C. ayresi*, described from three specimens newly-collected in the foothills of the Pico de Neblina range. They considered *C. ouakary* to be a junior synonym

of *C. melanocephalus* but, confusingly, chose to rename the nominal subspecies, rather than the junior synonym. Under this scheme, the new name for *C. ouakary* (*sensu* de Figueredo) became *C. melanocephalus,* while *C. melanocephalus* (*sensu* de Figueredo) was renamed *C. honshomi*. Studies by Ferrari *et al.* (2009, 2010, submitted) showed that i) *C. ouakary* is the valid name for the golden-backed populations of black-faced uacari, ii) that the most appropriate name for populations north of the Rio Negro is *C. melanocephalus,* and iii) that there is insufficient evidence to consider *ayresi* to be a full species, and it can, at best, be regarded as a sub-species of *C. melanocephalus, C. m. ayresi.* However, as this has yet to be published in a manner that meets the International Code of Zoological Nomenclature for a valid description it cannot be used as the valid basis for a taxonomic opinion (similarly, a thesis, such as Figueredo [2006] is; alone, also inadequate). However, arrangement of Ferrari et al (2010, submitted) is followed here for black-faced uacaris as I believe it permits the clearest comparative reading of the available literature on blackfaced uacaris. Hershkovitz (1987a) is followed for red-faced uacaris. For all other primates mentioned in the text the names are those given in Groves (2001).

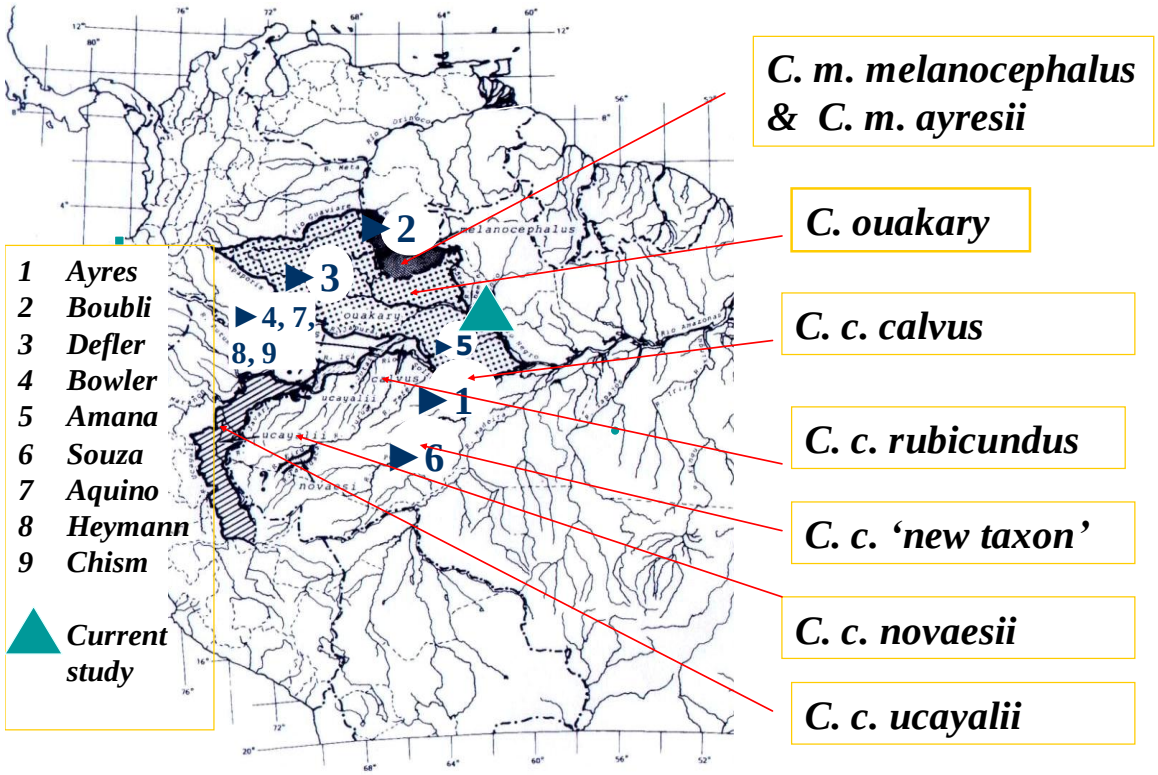


Fig. I-1: Distribution* Cacajao *taxa and previous study sites

1.3 Characteristics of *C. melanocephalus ouakary* – external appearance, morphology and anatomy

1.3.1 External Appearance

Adult golden-backed uacaris weigh around 3 kg. The facial skin is naked and black, as are the ears. The head is covered with black hair, as are the shoulders and arms. On the upper back the hair is pale yellow, while the flanks, tail and thighs are a rich cinnamon brown. The lower parts of the hind limbs have black hair. The belly is very sparsely haired, as are the hands and feet. The skin of all three regions is black. The hair is generally long and coarse, and on the flanks and upper back may reach over 20cm long, forming a Colobus-like cape (see Frontispiece).

The tail in all *Cacajao* species is short, less than one-third the body length, a unique feature among Neotropical primates. However, while not prehensile, the tail is not

inflexible, and retains the ability to curve (Barnett, pers. obs.). It may also be wagged in either the vertical or horizontal plane. Tail wagging, a possible displacement activity, appears to be largely confined to Pithecines among Neotropical primates (van Roosemalen *et al*., 1981 for *Chiropotes albinasus*; Fernandes, 1993 for review).

With the exception of some individuals with a black tail tip (Barnett *et al.*, 2005b), there appears to be little individual variation in colour pattern in *C. m. ouakary*. There are, for example, none of the pale areas on the face that facilitate individual identification in *Brachyteles arachnoides* (e.g. Strier, 1991).Young are born with the adult colour pattern, including a small pale area on the back. However, of this area appears to increase with age. At Jaú clearly very old individuals have been observed with the dorsal surface almost entirely golden-yellow.

There is little sexual size dimorphism in the genus *Cacajao* (Table I-2). For *C. m. ouakary* there is also little difference between the sexes in overall appearance. Though field observations at Jaú (current study) suggest that, in comparison to adult females, adult males may have proportionally broader heads, narrower waists and more extensive areas of yellow on the back, these differences have yet to be quantified. These intra-sexual differences are much smaller than in other pitheciines. Some species in the related genus *Pithecia* (Hershkovitz, 1987b) show sexual dichromism, this is absent in all *Cacajao*. In *C. m. ouakary*, there are no paired muscle-filled swellings or bulges in the *temporalis* region of the head, as appear, respectively, in adult males of some *Chiropotes* species (Hershkovitz, 1985), and in males of *Cacajao calvus* (Hershkovitz, 1987a: and Fig. IV-5). In *C. c. ucayalii* Bowler (2007, and pers. com.) has found that presence of temporal swellings and a larger much bushier tail permit unambiguous identification of adult males.

In addition, male *C. c. ucayalii*, appear a lot more aggressive than male *C. m. ouakary* (Bowler, 2007), and can be identified individually in the field by the facial scars derived from intra-species combat. This was not possible in the current study, as *C. m. ouakary* is aggressive and such scarring appears to be very rare (and when it occurs, it is very slight).

In addition to the difficulties of identifying individuals, sexing adult *C. m. ouakary* is also difficult in the field. The external genitalia are not easily visible. In males the testes are proportionately small, non-pendulous and black. The un-erect penis is black. The surrounding belly skin is also black. The glans is bright pink, but behaviours associated with its display rarely occur. In females, the vaginal area is black and there are no colourful and pendulous enlargements as occur, for example, in *Ateles* and other Atelines. In both sexes the genital area is often concealed from view, either by the long cape-forming flank hair, or by shadow generated by it.

Table I-2: **C. calvus** ***and*** **'C. melanocephalus'** ***Head-&-body Lengths and Weights*** *

		Body Weight (g) (g)			***Head-and-Body length (mm)***		
Species*	***Sex***	***Mean***	***N***	***Date Source***	***Mean***	***N***	***Data Source***
C. calvus	M	3450	1	Ayres (1986a)	456	19	Hershkovitz (1987a)
C. calvus	F	2875	2	Ayres (1986a)	440	21	Hershkovitz (1987a)
C. 'melanocephalus'	M	3400	1	Ayres (1986a)	414	17	Hershkovitz (1987a)
C. 'melanocephalus'	F	2804	3	Ayres (1986a)	389	21	Hershkovitz (1987a)

***Note:** for some studies datawere collected when *C. m. ouakary* and *C. m. melanocephalus* were not recognised as separate taxa (i.e. Ayres, 1986a). However, Ayres' (1986a) data were collected directly from wild-shot animals, and their location makes it a near-certainty that the animals were *C. m. ouakary*. But Hershkovitz (1987a) does not give museum numbers for the museum specimens he used, data therefore may include information from both *C. m. ouakary* and *C. m. melanocephalus*.

1.3.2 Sketelal Features – tail, limbs, hands and feet

Other pitheciines have a long tail with between 25 (*Pithecia*) and 28 (*Chiropotes*) caudal vertebrae (German, 2005). In *Cacajao*, the reduction in tail length has been achieved by reduction in both size and number of the caudal bones, with the distal three being fused or nearly so. The number of elements appears to be variable, having been reported variously as 11, 15, 17 or 20 (Beddard, 1887; Forbes, 1881; Mivart, 1865; Schultz, 1969).

The uacari thumb is non-opposable, and the first two digits of the hand oppose the others (schizodactylous, *sensu* Youlatos, 1999). The hand can grasp small objects by pressure contact at the inter-phalangeal joint or thenar pad, using the thumb as a form of clamp (Napier & Napier, 1967), or using the thumb and index finger in tandem to oppose the remaining three (Candland & Bush, 1995). This 'pseudo-opposability' is a feature of Neotropical primates (Napier, 1961); 'true' opposability, where the thumb can be converged *via* an axial rotation to face the other digits, is poorly developed in New World primates in general. Schizodactyly facilitates the grasping of branches (Youlatos, 1999), but precludes fine digital manipulation (Candland & Bush, 1995; Christel & Fragaszy, 2000a). The effect of this on uacari foraging has yet to be investigated, though it is clearly an important potential limitation (Christel & Fragaszy, 2000b; Dominy *et al.*, 2004; Fragaszy & Crast, 2004).

The intermembral index (a ratio of forelimb to hindlimb length) is 8.186 ± 1.6 for *C. m. melanocephalus* (Boubli, 1997a). It has not been calculated for *C. m. ouakary*, but likely is similar. This ratio is indicative of quadrupedal movement with a tendency to vertical-clinging-and-leaping (Martin, 1990).

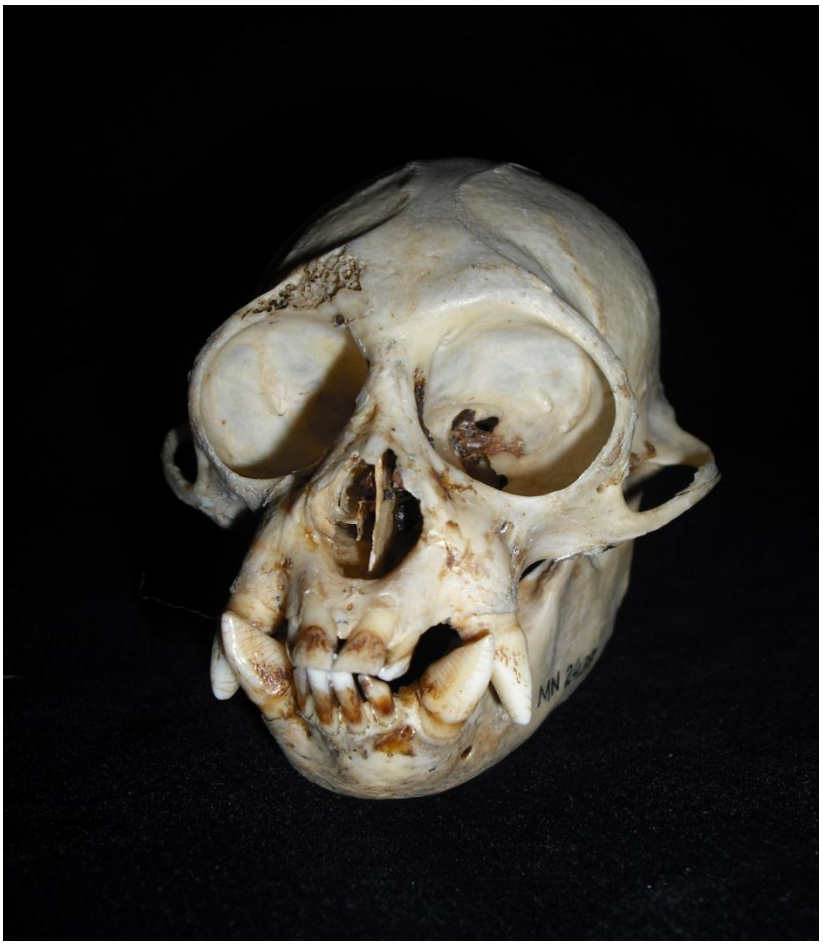
1.3.3 Cranial Features

Among Neotropical primates, pitheciines are the pre-eminent foragers on hard fruits, and cranium, mandible and teeth have all been extensively modified to deal with such a diet (Anapol & Lee, 1994). Uacaris possess the most extreme form of the pitheciine pattern (Kinzey, 1992). The noticeably prognathous snout of uacaris is due to enlarged frontal and nasal bones which are functionally allied with the enlarged and highly modified incisors and canines (see below). *Cacajao* has, proportionally, the largest temporal and masseter muscles of any Neotropical primate (Cachel, 1979), and one of the largest condylar areas

of any primate (Smith, 1983; Smith *et al.*, 1983). Comparatively, the area for insertion of the masseter muscle is large, with the temple region of the skull being more flattened than in any other cebid (Elliot, 1913). The zygomatic arch is strengthened and moved forwards on the skull, a feature shown in several mammal groups where biomechanical advantage for increased bite force is required (Anyonge & Baker, 2006: canids; McHenry *et al.*, 2007: felids; Sacco & Van Valkenburgh, 2004: ursids; Iuliisa *et al*., 2000: xenartha).

The jaw of *Cacajao* (and other pitheciines) is also characterized by a general robusticity (Anapol & Lee, 1994), a symphysial region that is especially thick, deep, robust, firmly-fused, and also widened, resulting in mandibles with parallel sides (a U-shape: Kinzey, 1974). These features resist the mechanical compression associated with repeated use of large dental forces against large hard objects (Kinzey, 1974; Smith, 1981, 1983). Non-pitheciine cebids, in which only *Cebus* regularly process hard food objects dentally (molars only), have more V-shaped mandibles (Anapol & Lee, 1994), and a more gracile symphysial area.

The teeth of all uacaris are also highly specialized. A wide diastema separates the lower canines from lower incisors (Seth & Seth, 1986). The incisors are large, laterally splayed (Fig. I-2) and triangular in cross-section (Hershkovitz, 1987a). The dental formula for uacaris is typical for a large Neotropical primate: 2 1 3 3 // 2 1 3 3



Adult female, Museu Nacional, Rio de Janeiro, Brazil.

***Fig. 1-2: Skull of* Cacajao melanocephalus ouakary**

Large enough to distort the exterior facial skin (Fig. I-3), *Cacajao* canines are proportionately among the largest canines of any primate (Smith, 1981). Leutenegger (1982) found little sexual dimorphism in canine size in *Cacajao*. Kay *et al*. (1988) believe this to be associated with low levels of physical competition between males for mates. In such species such as *Papio* and *Theropithecus* baboons, canines are used in inter-male aggression (e.g Walker, 1984), but, in contrast, uacari canines appear to be purely dietary specializations, with no role in sexual display (Greenfield & Washburn, 1991; Kay *et al*., 1988; Smith, 1981). Eaglen (1984) reported that, at 14mm long, uacari incisors are, proportionately, among the largest of any New World primate and posited that this related

to a diet dominated by hard-shelled fruits, requiring the separation of husk from pulp and seed by incisal preparation. This is aided by the incisors' marked procumbency and by the scoop-like form of their adpressed crowns (Kay, 1990; Kay *et al*., 1988), which together act as a highly efficient nipping, cropping or gouging device (Kinzey, 1992**).**

Large and extremely robust, uacari canines are highly, and subtly, modified for a hard fruit diet (Kinzey, 1974, 1992). A lower buccal cingulum is present, a character related to shearing of each upper canine tooth against the corresponding lower anterior premolar, a feature termed 'canine honing' (Kinzey, 1974). The lower canines bear a strong flange on their inner surfaces that, chisel-like, occludes with the mesial surface of the corresponding upper canine (Kay, 1990), facilitating penetration of food objects. *Cacajao* canines are also strong and highly resistant to bending. An analysis by Plavcan & Ruff (2008) found teeth of *Cacajao* to be the strongest of any of the 114 primates tested and, for the 45 sampled carnivores, were exceeded in strength only by wolves, hyaenas and big cats.

The posterior teeth, the premolars and molars, are square and relatively small, with low-relief cusps. Unlike species that process hard foods with their molars (e.g. *Cebus apella*: Martin *et al*., 2003), uacari molars do not have thick enamel. They do, however, possess extremely well-defined Hunter-Schrager Bands, the result of decussation of the enamel prisms. Hunter-Schrager Bands are an epiphenomenon, and while they do not themselves strengthen the tooth, they indicate that the dentine is prismatic and that the enamel columns are organized in a way which maximizes strength and minimizes crack propagation (Bajaja *et al*., 2008; Todd Rae, pers. comm.). Martin *et al.* (1994) originally reported densely-packed enamel prisms, believing these resisted the forces generated during dental processing of hard foods by uacaris. However, the packing is not markedly

denser than in other cebids that were reported on by Nogami & Yoneda (1983). This is because uacaris use their anterior teeth to process hard fruit and seed exteriors, whereas molars just process relatively soft seed interiors. I confirmed this with personal observations of *Cacajao calvus rubicundus* in Rio de Janeiro Primate Centre. Following an analysis of wear facets and cusp cavitation patterns, Hagura (1994) suggested that *Cacajao* molars were used as grinders and, unlike other cebids (notably *Cebus*) did little puncture-crushing during food preparation. Instead, as revealed by Kinzey's (1992) analysis of wear patterns, uacari molars mechanically triturate seeds that are elastic and resilient as opposed to hard and brittle. The prominent crenellations on the surface of uacari molars may act to contain deformation of such seeds during trituration (Kinzey, 1992). In uacaris, molar wear is probably resisted by their low occlusal relief (Rosenberger & Kinzey, 1976).

Adult male, Rio de Janeiro Primate Centre *Photo: Bruna Bezerra*

***Fig. 1-3: The Head of* Cacajao melanocephalus ouakary**

1.3.4 Soft Anatomy

Comparing the various parts of the uacari alimentary canal, Ayres (1989) noted that while the stomach comprises 5-8% of total gut surface area and is relatively small, the caecum occupies some 60-70% of the digestive tract's total area, and is thus relatively large. The caecum may be up to 25cm long (Flower & Lydekker, 1891). MacLarnon *et al*. (1986) reported on the allometry of the gastrointestinal tract in *Cacajao* (including *C. melanocephalus* – a taxon which, at the time, included *C. m. ouakary*). A comparative approach allowed them to produce a graphic model that predicted the importance of folivory for species where diet was, at the time, essentially unknown. Based on these results, which placed uacaris in the 'partial folivore' section, they proposed that *Cacajao* engaged in mid-gut fermentation of leaves. It is now thought that the enlarged colon is related to seed fermentation (Ayres & Chivers, unpublished), though the report by Barnett *et al*. (2005a) of seasonal folivory in *C. m. ouakary* may mean that this organ functions differently in different seasons (as do the intestines, for example, of songbirds with great inter-seasonal variations in diet: e.g. Stanley & Lill, 2002; Whelan & Brown, 2005). This would correspond with the more recently recognized high level of biochemical flexibility of the primate digestive tract (e.g. Lambert, 1998).

1.4 Uacari Biology

1.4.1 Previous Field Studies of the Genus Cacajao

This is the first long-term study specifically devoted to studying the diet and feeding ecology of the golden-backed uacari. However, there have been studies of other members of the genus which can, with reservations concerning differences in composition, productivity and phenology of the habitat, serve as useful comparisons and reference

points for the current study. The study topics of these and the locations at which the studies were carried out are presented in Table I-3.

***Table I-3: Chronology of Previous Field Studies of the Genus* Cacajao**

Author	***Taxon***	***Years of Activity***	***Sample Publication***	***Activities***	***Location***
Russell A. Mittermeier	*Cacajao*	1974	Mittermeier & Coimbra-Filho (1977)	Field surveys, estimates of hunting impacts, general natural history data and questionaires	Rios Negro Solimoes and tributaries, Brazil
Roy Fontaine	*C. c. ucayalii*	1978	Fontaine (1979)	Field observations on habit, habitat use, and behaviour	central-Río Ucayali, Peru
J. Marcio Ayres	*C. c. calvus*	1983-1984	Ayres (1986a)	Quantitative studies of diet, ranging and habitat use in relation to phenology. Some social behaviour.	Lake Teiú, Mamirauá, Rio Solimões, Brazil
Rolando Aquino	*C. c. ucayalii*	1985-1996	Aquino (1988, 1998)	Quantitative and qualitative data on habitat use, ranging, group size, social behaviour, hunting impacts and interactions with other species	Río Ucayali and tributaries, Peru
EckhardHeyman Ursula Bartecki	*C. c. ucayalii*	1985 - present	Bartecki & Heymann (1987), Heymann (1987, 1992a)	Field surveys, quanitative observations on diet, habitat use group size and general behaviour	Quebrada Blanco, Río Ucayali. Peru.
Adrian Barnett Aléxia da Cunha	*C. m. ouakary*	1989	Barnett & da Cunha (1990), da Cunha & Barnett (1990).	Field surveys, quanitative observations on diet, habitat use, group size and general behaviour	rios Curicuriari and Uaupes, tributaries of upper Rio Negro, Brazil
Thomas Defler	*C. m. ouakary*	1989-1995	Defler (1991, 2001)	Quantitative data on habitat use, ranging, group size and interactions with other species	Capurú, Río Apaporis, Colombia
Shaun Lehman	*C. m. melanocephalus*	1992	Lehman & Robinson (1994a,b)	Field surveys, quanitative observations on diet, habitat use, group size and general behaviour	Tributaries of Río Orinoco, Amazonas State, Venezuela
Jean-Philippe Boubli	*C. m. melanocephalus*	1993-1994	Boubli (1997a, 1999)	Quantitative studies of diet, ranging and habitat use in relation to phenology. Some social behaviour.	Pico de Neblina National Park, Brazil

Table I-3: Field Studies of the Genus* Cacajao- *continued 1

Author	*Taxon*	*Yeaes of Activity*	*Sample Publication*	*Activities*	*Location*
Cynthia Bennett, Suzie Leonard	*C. c. ucayalii*	1993-1995	Bennett *et al.* (2001), Leonard & Bennett (1995, 1996)	Observations on sleeping trees, daily ranging, feeding behaviour, interactions with other species.	Tributaries of the upper Ucayali, Peru
Suzanne Walker	*C. c. calvus*	1992-1994	Walker & Ayres (1996)	Positional behaviour of white uacaris	Mamirauá, Rio Solimões, Brazil
Carlos Peres	*C. c. novaesii*	1996	Peres (1997)	Field survey, brief notes on habitat use and behaviour	South-western Amazonia
Janice Chism and students	*C. c. ucayalii*	2000	Swanson-Ward & Chism (2003)	Observations on sleeping trees, daily ranging, feeding behaviour.	Tributaries of the upper Ucayali, Peru
Adrian Barnett and collegues	*C. m. ouakary*	1999, 2000, 2005	Barnett & de Castilho (2000), Barnett *et al.* (2000, 2005a)	Field surveys, qualitative and quantitative observations on diet, competitors, habitat use and general behaviour	Rio Jaú, Jaú National Park, Brazil.
Mark Bowler	*C. c. ucayalii*	2003-2005	Bowler (2007), Bowler & Bodmer (2009)	Quantitative studies of diet, ranging and habitat use in relation to phenology. Studies of potential competitors, social behaviour and conservation assessments also conducted.	Lago Preto, Río Yavarí, (Ucayali tributary), upper R. Ucayali, Peru.
Helder Queiroz and students	*C. m. ouakary*	2004-2006	Barnett *et al.* (in press)	Stuies of diet in relation to phenology and habitat use. Study of hunting patterns of local human communities an their impact on uacari populations	Amanã Sustainable Development Reserve, Brazil
Bruna Bezerra	*C. m. ouakary* (following taxonomy of Boubli et al. and therefore reported as *C. melanocephalus*)	2007-2008	Bezerra (2010)	Quantitative studies of vocalizations, social biology. Data on ranging, foraging, interactions with other species	Rio Jaú, Jaú National Park, Brazil.

Four of the above studies conducted for Doctoral theses. Three provided methodological guidance for the current study. These were: an 18-month investigation of

the ecology of the white bald uacari (*Cacajao calvus calvus*) by J. Marcio Ayres in the seasonally-flooded whitewater forests (várzea) of Lake Teiú-Mamirauá on the Rio Solimões, Brazil (Ayres, 1986a,b, 1989); a broad-based study of the ecology of *C. m. melanocephalus* undertaken across 17 months by Jean-Philippe Boubli (1994, 1997a,b, 1999) in the caatinga (a non-flooded forest type growing on especially poor soil) in the Pico de Neblina region of the upper Rio Negro, Brazil, and a 12-month study of the Peruvian red uacari (*C. c. ucayalii*) by Mark Bowler, based at Lago Preto on the Yavarí river, Peru (Bowler, 2003, 2007; Bowler & Bodmer, 2009), and conducted in terra firma, palm swamp and várzea. The field localities are marked on Fig. I-1. The fourth study (Bezerra, 2010) was conducted in tandem with the current study, and my work beneffited considerably from the resulting interchange of ideas.

In addition, a series of ecological studies of *C. c. ucayalii* have been conducted by Peruvian primatologist Rolando Aquino and colleagues, covering diet, daily and seasonal range and habitat choice of this primate (Aquino, 1988, 1995ab; 1998; Aquino & Encarnación, 1994, 1999). These topics have also been investigated for *C. c. ucayalii* by Eckhard Heymann and colleagues (Bartecki & Heymann, 1987a; Heymann, 1989, 1990, 1992a; Heymann & Aquino, 2010), Leonard & Bennett (1995, 1996), and Swanson Ward & Chism (2002). Suzanne Walker conducted a 6-month field investigation of the white bald uacari (*C. c. calvus*) for a study of postural behaviour (Walker, 1996; Walker & Ayres, 1996). A short survey of Venezuelan blackwater flooded forests (igapó) was conducted by Lehman & Robertson (1994a,b) for *C. m. melanocephalus* (this remains the only recent study of the ecology of this taxon in Venezuela – previous data by Handley

[1976] presenting only the collection localities of shot specimens). Study sites locations appear in Fig. I-1.

The reports of studies on a semi-free ranging population of red uacaris at the Miami Monkey Jungle (Fontaine, 1981; Fontaine & Du Mond, 1977; Fontaine & Hensch, 1982) continue to be a source of useful information. As with a study of parental care (Cox et al., 1987), the uacari sub-species in these studies given as *C. c. rubicundus*, though the animals clearly come from Peru, which is at the westrn margin of the range of *C. c. rubicundus*. This occurred because the studies were published before Hershkovitz (1987a) clarified the the status and distribution of these two taxa. Accordingly, it is now generally agreed (e.g. Barnett & Brandon-Jones, 1997; Bowler, 2007) in these studies is what is now known as *C. c. ucayalii*.

To date there have been no detailed studies of neither *C. c. rubicundus* nor *C. c. novaesi* due to the lack of an appropriate study site where animals can be encountered with sufficient consistency to be habituated. To date work on these animals has been restricted to surveys of population density and geographic distribution (e.g. Peres, 1988 on *C. c. novaesi*; Vieira et al., 2008 on *C. c. rubicundus*). Silva Jr. & Martins (1999) provided field data on what may be a new taxon of white-haired *C. calvus.*

Susceptibility to hunting has been studied for *C. c. calvus* by Peres (1990a, 1997, 2000a), by Chism & Matthews (2006) for *C. c. uacayalii*, and by Fleck & Bodmer (2005) for *C. m. ouakary*. A study of the ecological role of *C. calvus* in primate communities of the western Amazon, has been undertaken by Peres (1988, 1997), Peres & Dolman (2000) and Peres & Palacios (2007).

1.4.2 Previous Field Studies of **Cacajao melanocephalus ouakary**

The golden-backed uacari does not appear to do well in captivity (Schmidt, 1985; Whitehead, 1984), and there have been no reported studies of their physiology, feeding or social behaviour in zoos or other institutions, to equal those of Fontaine on red uacaris. There have also been few previous field studies specifically devoted to *C. m. ouakary*.

In Brazil, some short field surveys of primates conducted in the Rio Jaú area by Anthony Rylands in 1991 (Rylands, 1992), along the lower Rio Negro by Russell Mittermeier (Mittermeier & Coimbra-Filho, 1977), and of the Amanã Ecological Reserve by Amaral *et al.* (2005), all included qualitative ecological observations of *C. m. ouakary.* Short-term studies focussed specifically on golden-backed uacari diet and habitat preferences were conducted by the author and Aléxia C. da Cunha on tributaries of the upper Rio Negro (Curicuriari and Uaupés rivers) in 1989 (Barnett & da Cunha, 1990, 1991; da Cunha & Barnett 1990). As a prelude to the current study, short surveys were conducted in 1999 (the author with Carol V. de Castillo), 2000 (the author with Rebecca L. Shapley) and 2005 (the author with Adrian Deveny and Verena Schiel) in Jaú National Park, Amazonas, resulting in notes and papers concerning general observations on diet and habitat preferences of the golden-backed uacari (Barnett *et al.*, 2000, 2002, 2005a,b,c), and predation upon them (Barnett *et al*., in press). Data from a preliminary study of dietary overlap between parrots, macaws and uacaris at Jaú is presented by Almeida *et al.* (2008). Research into the vocal and social behaviour of the golden-backed uacari, was conducted contemporaneously to the current study at Jaú by Bruna Bezerra, for her PhD (Bezerra, 2010). Data presentations from this study include Bezerra *et al.* (2007, 2008, 2010abc).

In Colombia, Thomas Defler has been studying golden-backed uacaris intermittently since 1989. Conducted as part of a general study of primate ecology of the Río Aparpornis, the fieldwork has not focused specifically on uacari. Interrupted by civil war, Defler was forced at gun-point from his research station, all his notes and records were burnt and the the habituated study animals shot. Nevertheless, a number of key papers have come out of the study area including publications on diet (Defler, 1991), fission-fusion sociality (Defler, 1999), population densities (Defler, 2001), and comparison with other *C. m. ouakary* study sites (Barnett *et al*., in press a). Other, previously unpublished data on diet and behavioural ecology of *C. m. ouakary* in Colombia are presented in Defler (2004). The distribution of these study sites is given in Fig. I-1.

Analysis of susceptability to hunting has yet to be undertaken for *C. m. ouakary,* though both species have been included in the analysis of the biological and environmental determinants of primate community structure by Peres & Janson (1999).

1.4.3 Known distribution of Cacajao melanocephalus ouakary

The known outline distribution of *Cacajao m. ouakary* is included in Fig. I-1. This is a historical distribution based on museum specimens and follows that given in Hershkovitz (1987a). However, complete occupation of the area is unlikely. It is more plausible that the actual distribution is patchier, reflecting both the distribution of appropriate habitat and the impacts of past hunting (a situation similar to that noted by Chism & Matthews [2006] for *C. c. ucayalii*). The fieldwork has yet to be done to finalize the western and northern limits of the species range. The southern limit, the northern bank of the Solimões, is fairly certain. The eastern-most distribution has yet to be fully determined, through is unlikely to extend to the tip of the Negro-Solimões interfluve as it did in historical times,

due to the growth of towns, agriculture, cattle rearing and associated infrastructure in this region. There are, however, still populations of *Cacajao m. ouakary* in the Manacaparu region, (Wilson Spironello, pers. comm. of pers. obs.), in the far west of the Negro-Solimões interfluve. The future survival of these animals is likely to be threatened by the human population expansion that will follow the construction of a bridge over the Rio Negro at Manaus (Vieira Sá *et al*., 2010). An unpublished study by Simone Iwanaga (Iwanaga, pers. com.) found very low primate densities to the immediate east of the Rio Carabinani and the eastern boundary of Jaú National Park (locality 10, Fig. I-1). It is very possible that the populations of golden-backed uacari within this protected area are the species' eastern-most viable populations.

1.4.4 Habitat and Habitat Preferences

The distribution of *C. m. ouakary* is coincident with that of the black-water river system of the Rio Negro and the affluents of its blackwater drainage basin. Here *C. m. ouakary* spends up to nine months of the year in the seasonally-flooded forests along the river margins. Riverside forests are a feature of all minimally-disturbed parts of the Amazon basin. Their form, extent, topology and community structure are all intimately tied to that of the regional geology. For the Rio Negro basin, proximity to the Guyana Shield means that the underlying rocks are generally very ancient (often Pre-Cambrian) and erosion resistant. Consequently, clays are rare, soils are often based on white sand and the sediment load of blackwater rivers is therefore very slight (Goulding, 1990; Goulding *et al*., 1996). This is in marked contrast to the situation on the Solimões and its affluents, a river system that has its origins in the easily erodable volcanic deposits of the Andes, and which, as a result, are rich in suspended sediments (Goulding, 1990; Goulding *et al*.,

1996). The beds of blackwater rivers tend to be V-shaped, while those of white-water ones tend to be in the form of a very broad and open U.

Because of this difference in slope, black-water rivers provide narrow (often less than 200m wide) floodplains for rivermargin forest, while floodplain forests on the margins of whitewater rivers may be several km in width. The seasonally flooded rivermargin forests on blackwater systems are called *igapó*, while those on whitewater systems are known as *várzea* (Prance, 1979). Tree species of the rivermargin forests differ in their tolerances to inundation (Parolin, 2000a,b). Some (e.g. *Amanoa oblongifolia* and *Hevea spruceana* - both Euphorbiaceae) are able to withstand up to 11 months of partial inundation and 6 months of complete submersion. Others (e.g. *Aldina heterophylla*, *Macrolobium acaciifolium* and *Swartzia acuminata* – all Fabaceae) cannot survive more than 2-3 months of having their roots completely covered by water (Parolin, 2000a,b). Because flood levels are annually predictable events that vary little in extent and timing (Goulding *et al*., 2003), a combination of slope rate, inundation duration and variation in physiological tolerance to flooding between tree species, produce within-community tree species' distribution patterns that are strongly banded. The growth and flooding tolerance of the seedlings and adult trees are reflected in a zonation of tree species along the inundation gradient, with tolerant species growing on lower levels, and less tolerant species growing on higher levels (Ferreira, 2000). Consequently, sub-communities of species with similar tolerances occur in bands parallel to the shore (Ferreira, 1997). In contrast to the duration of inundation-driven horizontal stratification of the igapó, the várzea (flooded forest on white water rivers) is, because of sediment load, rather more of a mosaic, with patterns of tree species distributions following the complex of sloughs and

levees that characterize the region (Ayres, 1986a; Ferreira, 1997; Goulding *et al.*, 2003; Parolin, 2000a,b), and on which grow restinga (levée) and chascavel (swamp) vegetation, respectively. The contrasts of the the two habitats may be seen in Figs. I-4 a.

Golden-backed uacaris were originally thought to live only in igapó (e.g. Mittermeier & Coimbra-Filho, 1977). However, later work established that their presence there was seasonal (Barnett & da Cunha, 1991; da Cunha & Barnett, 1990), and that, although *C. m. ouakary* spend the majority of the year in igapó, individuals migrate to immediately contiguous terra firma rainforest for part of the year (Barnett *et al.*, 2005a; Defler, 2001), though the extent and duration of this may vary between sites (Barnett *et al*., in press). For reasons which are currently unclear, golden-backed uacaris appear to avoid várzea – even in white-water areas where there is no possible competition from *C. calvus* (a várzea specialist). This avoidance appears to be quite complete: Rylands (1992) reports golden-backed uacaris were absent from a white-water river in an otherwise uacari-rich area of black-water rivers, while in the southern part of the Amanã Sustainable Development Reserve, where white- and black-water systems interdigitate, golden-backs are found in igapó, and Brazilian red uacaris (*C. c. rubicundus*) in várzea (Amaral *et al.*, 2005; S. Borges pers. comm.).

Igapó interior, Jaú Igapó exterior , Jaú

Fig. I-4: Igapó Forms a Narrow Band of Flooded Forest along the River Margin

Várzea, Rio Solimões

Fig. I-5: Várzea from the Air, Showing Broad Floodplain and Characteristic Striated Pattern of Restinga (Levée) and Chascaval (Swamp) Vegetation Types

Though Brazilian populations of *C. calvus* appear to spend more time in várzea than any other habitat (Bowler, 2007; Silva Jr. & Martins, 1999), Peruvian populations on the Río Uacayali and its tributaries behave differently – moving through a habitat mosaic of terra

firme, flooded forest and palm swamps (Heymann & Aquino, 2010). Use of the habitat types coincides with peak fruit abundance of one or more tree species (Bowler, 2007).

1.4.5 Diet, Feeding Ecology and Foraging Behaviour

Until the current study there had been no quantitative long-term study of the golden-backed uacari diet. The only observations of foods of the species in Brazil had been published by da Cunha & Barnett (1990), Barnett & da Cunha (1991) and Barnett *et al.* (2005). The first two papers mentioned that *C. m. ouakary* ate seeds of *Swartzia* sp. (Fab.: Pap.), and two species of Sapotaceae, while the later paper reported the diet to include fruits, insects as well as a variety of young leaves (*Buchenavia oxycarpa*: Combretaceae, *Eschweilera tenuifolia*: Lecythidaceae, and *Mabea taquari*: Euphorbiacae) in the dry season when little fruit was available. For Colombian populations of *C. m. ouakary*, Defler (2004) reports seeds (mature and immature), fruit pulp, arils, and flowers from 17 species in 12 families. He does not report insectivory.

Mechanical interpretations of the cranial morphology of the genus *Cacajao* had led to the expectation that uacaris would be 'sclerocarpic foragers', with a high incidence of immature seeds in their diet that would come from fruits that were hard-husked (Kinzey, 1974). The seeds would be separated from the husk using a two-stage processing format that involved separation of seeds and husk by the large splayed canines and removal of the seed (entire or in fragments, depending on its size) by the procumbent incisors (Kinzey, 1974). This museum-based interpretation received field support with the first long-term studies of wild uacaris. Ayres (1986a,b, 1989) recorded 100 species in the diet of *C. c. calvus.* Within this, seeds (mostly from hard-husked fruits) constituted 67% of the diet. Aquino & Encarnación (1999) reported *C. c. ucayalii* eating 53 plant species from 20 families, of which 46% were consumed for their seeds. Of these 67% were surrounded by

thick heavy husks and were consumed in an immature state. In the dry season, Peruvian red uacaris will also eat bromeliad leaf bases (Aquino, 1995), and they also move to unflooded forest to feed on palm fruit (Aquino & Encarnación, 1994) as well as (unspecified) flowers and leaves. Bowler (2007) recorded 164 plant species in the diet of *C. c. ucayalii* on the Yavarí river, Amazonian Peru, though only 22 constituted more than 1% of the recorded annual diet. The species most eaten was the palm *Maurita flexuosa*, the pulp of its fruit providing nearly 20% of feeding records. In total, some 37% of the diet was ripe pulp (mostly from *Mauritia*). Unripe seeds constituted 50.6% of the recorded diet, with *Licania heteromorpha* (Chrysobalenaceae), *Couma macrocarpa* (Apocynaceae), *Chrysophyllum sanguinolentum* (Sapotaceae) and *Hevea* cf. *guianensis* (Euphorbiaceae) being the most important contributors. At the generic level, 23 genera contributed some 74% of feeding records and 16 families constituted over 80% of feeding records. Areceae, Sapotaceae, Fabaceae and Lecythidaceae were (in that order) the four most eaten families. Vine fruits were important in some months, when they constituted up to 10% of diet records. Selectivity was high – with 15 genera being eaten at frequencies greater than they occurred in the environment and 16 at lower than expected frequencies. Six of the 10 most eaten fruits were classified (qualitatively) as either hard or very hard. At 1.7%, faunivory was a minor diet component, with ants, caterpillars, termites, mantids and katydids recorded as being eaten. Bowler (2007) considered his figures for insectivory to be an underestimate, especially as 3.4% of scan time was taken up with searching in foliage (presumably for insects). Flowers (especially of *Eschweilera*) were seasonally important and, overall, constituted 3.4% of the feeding records for *C. c. ucayalii* at Lago Preto.

The known *C. m. melanocephalus* diet (Boubli, 1997a) has 89% fruits, 5% flowers, 4% leaves and leaf parts and 2% invertebrates. Fruit were eaten from 95 species of trees and 25 species of liana. Of these 120 species, 23% had soft fruits, 77.8% were consumed for their seeds and 63.8% of feeding records were of unripe seeds. Defler (2004) calculated that 93% of the species he recorded in the diet of *C. m. ouakary* in Colombia were eaten for their seeds, and 7% for their pulp. Many of the hard-husked fruits were also immature, 82% in the case of *C. c. calvus* (Ayres, 1986a, 1989), 67% in the case of *C. m. melanocephalus* (Boubli, 1997a). Boubli (1999) reported that the fruits of the three most frequently-eaten species (*Micrandra spruceana* and *Hevea brasiliensis* - both Euphorbiaceae, and *Eperua leucantha*: Fab.: Caes.) had heavily-armoured fruits, and that they were foraged on in proportion to their frequency in the environment. Ayres (1986a,b) reached similar conclusions for *C. c. calvus* (though the eaten species were different).

However, fruits and their seeds were not the only eaten items. Boubli (1997a) reported that *C. m. melanocephalus* also consumed ripe fruit and arils, young leaves, bromeliad leaf bases, petioles, whole flowers, stamens and nectar. Similarly, for *C. c. calvus,* Ayres (1986a) reported that, in some months, fruits made only a minor contribution to the diet. For example, during the dry season at Teiú-Mamirauá, the flowers of *Eschweilera turbinata* (Lecythidaceae) constituted up to 60% of the monthly diet records. Insectivory has been recorded at low levels – Ayres observed that *C. c. calvus* would seasonally eat considerable volumes of caterpillars, while katydis and cockroaches were reported for *C. m. melanocephalus* by Boubli. Though the texts do not specify, this appears to be active insectivory. The role of protein uptake *via* passive ingestion of insect larvæ inside eaten fruits or seeds does not appear to have been studied previously for the genus *Cacajao.*

However, studies of red titi, *Callicebus cupreus*, by Tirado Herrera & Heymann (2004), found not only does this occur, but that it does so more commonly in infant-raising females. Preliminary observations on *C. m. ouakary* (Barnett *et al*., 2005a), found that up to one-third of eaten fruit types were either small, thin-skinned or both. During the dry season fruit dearth, *C. m. ouakary* ate quantities of young leaves from *Buchenavia oxicarpa* (Combretaceae), *Eschweilera tenuifolia* (Lecythidaceae) and *Mabea taquari* (Euphorbiaceae).

Data on diet item availability were quantified by Ayres (1986a,b) for *C. c. calvus* and by Boubli (1997a) for *C. m. melanocephalus* in terms of plant phenology and the relative abundances of tree species in study quadrats. Crop volume was not quantified in either case, nor did these authors consider such modifying factors as the presence of plant defences (spines, latex etc.) or symbiotic associations with ants.

Some of the fruits used by *C. m. ouakary* are so exceedingly hard that I found the easiest way for a human to open them was to use a hammer. Broken teeth generally have sub-optimal biomechanical efficiency and may act as entry point for infection (Crovella & Ardito, 1994; Curtis *et al*., 1986; Sauther *et al.*, 2001). Such infections can be extremely debilitating for wild mammals (e.g. Baldus, 2006; Cuozzo & Sauther, 2004). Studies of large-toothed mammalian predators such as Smilodontine cats (van Valkenburgh, 2001), have revealed they foraged in ways that minimized the likelihood of dental damage. In spite of this, the manner in which fruits are opened and its significance for foraging has not been dealt with for any member of the genus *Cacajao*. There has been no previous study that has looked at exactly how uacaris open fruits, whether this varies between fruit morphologies and, if such variation exists, what causal factors might explain it.

1.4.6 Competition

The level of competition between *C. m. ouakary* and potential competitors has not previously been investigated. Competition between congenerics is unlikely as they are separated by either habitat or geographical range. This is also largely true of *Cacajao* and *Chiropotes*, with only one small area of overlap having been recorded - in the Pico de Neblina region of Brazil (Boubli, 2002). Furthermore, as Barnett *et al*. (2005) have noted, recording two specialist taxa in sympatry does not indicate they compete extensively, since this may be limited to rare resource bottlenecks, and even then the populations involved may simply migrate elsewhere. Members of the genus *Pithecia* are sympatric with *Cacajao* across its entire Amazon basin distribution, but *Pithecia* are smaller, rarely enter igapó (Peres, 1993), have a lower proportion of large hard fruit in their diet (Norconk, 1996; Setz, 1987) and make greater use of the forest's lower and middle stories (Norconk, 2007).

Direct resource competition is possible between *C. m. ouakary* and other arboreal hard fruit seed predators (e.g. squirrels, parrots and macaws), and has been reported for *Chiropotes* and macaws (Norconk *et al.*, 1997), and for *Pithecia* and macaws (Palminteri *et al.*, in press). Barnett *et al.* (2005a) report that at Jaú, golden-backed uacaris, macaws and parrots had three seed-source trees in common, and dietary overlap between squirrels and golden-backed uacaris, but did not provide any quantified evidence of competition. Bowler (2007) notes that, at Lago Preto, apart from *C. c. ucayalii*, the only other primate feeding on unripe seeds during the study period was *Pithecia monarchus*, though a lack of correlation between their abundances across four sites does not argue for strong competition. Negative correlations between abundance of red uacaris and arboreal

(*Sciurus* spp.), and terrestrial (*Dasyprocta fuliginosa*) rodent seed predators may, however, indicate some competitive interactions (Bowler, 2007).

1.4.7 Movement

Cacajao calvus and *C. m. melanocephalus* are generally arboreal quadrupeds (Boubli, 1997a; Walker, 1996; Walker & Ayres, 1996), with walking, running, clamber-running, leaping and bridging in the upper and middle-upper levels of the forest canopy commonly being observed. Arm-swinging and bipedal branch walking have been observed, and pedal suspension to reach branches or food items has also been recorded for both *C. calvus* and *C. m. melanocephalus*. *C. calvus* has been observed descending to the ground to feed on germinating Sapotaceae seedlings, while *C. m. ouakary* has been filmed raiding the nests of freshwater turtles (Barnett, 2005). The canopy movements of the golden-backed uacaris have not been quantified prior to this study, but qualitative ethograms suggest a pattern of locomotion and canopy strata use similar to that employed by *C. c. calvus* and *C. m. melanocephalus* (Boubli, 1997a; Walker, 1996; Walker & Ayres, 1996). Despite the short tail, frequent leaping, often across wide gaps, has been reported from all studied taxa of uacaris (Boubli 1997a; Walker 1996; Walker & Ayres 1996). This includes *C. m. ouakary* for which Barnett *et al*. (2007) reported a leap of 13m. Such capacities doubtless reflect adaptations to the relatively discontinuous nature of the canopy of their forest habitat (see Walker, 1996). Golden-backed uacaris have been seen swimming (Barnett *et al.*, 2007); this has not yet been reported to date for other uacari taxa.

1.4.8 Time Budget

There are no published data on time or activity budgets for *C. m. ouakary*. Annual averages for the closely-related black-backed uacari by Boubli (1997a) were made in a very different habitat than that occupied by *C. m. ouakary*, one that varies in both the

nature of the canopy and the distribution of resources in both time and space. For these reasons, these data may not be a good guideline to golden-backed uacari time-budgets. For *C. m. melanocephalus*, Boubli (1997a) also observed that most travel and most moving-foraging occurs early in the day and late in the afternoon, with resting in late morning and early afternoon, and he stated that, outside of these resting periods, feeding was distributed relatively uniformly throughout the day. This is a common pattern in primates (see, for example Defler, 1995: *Lagothrix*; Harrison, 1985: *Cercopithecus sabaeus*; Umapathy & Kumar, 2000: *Macaca silenus*), though some species may show feeding peaks at the start and end of the day (e.g. Chapman & Chapman, 1991: *Ateles*). For the white bald uacari, Ayres (1990) reported that begin feeding shortly after leaving their sleeping trees at dawn. They then fed until mid-day, when they rested. Feeding resumed in the mid-afternoon and continued until a new sleeping site was taken up around dusk. The nature of sleeping trees has not been recorded previously for either *C. m. ouakary* or *C. m. melanocephalus*.

Boubli (1997a) for *C. m. melanocephalus*, Bowler (2007) for *C. c. ucayalii* and Ayres (1986a) for *C. c. calvus* reported averaged annual time budgets dominated by moving and feeding. Ayres (1986a) noted that there were seasonal variations, with more time moving and less time resting in the high-water months. The large proportion of time spent moving is a reflection of the large range sizes of uacaris, which are associated with the low density and patchiness of food resources. This also explains the use of combined categories such as 'moving/foraging' by Boubli (1997a), as uacaris often grab food in passing on their way to larger patches (Barnett, current study).

Though there are some differences between uacari species in the relative proportions of the time budget categories, they are small when compared to the allocation patterns of other primates such as *Alouatta*, a folivore. Though similar in weight to *Cacajao*, *Alouatta* have smaller home ranges and spend much less time moving and foraging and more time resting, and a species such as *Cebus olivaceus* spends up to half its time moving and one-fifth foraging (e.g. Robinson, 1986), reflecting the intensive locale-specific searching for small diet items (often insects) that is characteristic of *Cebus* foraging (Fragaszy *et al*., 2004). The proportions of reported uacari time budget are, however, quite similar to other Neotropical primates that exploit large widely dispersed food patches, such as *Lagothrix* and *Ateles.*

1.4.9 Daily and Seasonal Ranges

To date there is little published information on the daily and seasonal ranges of the golden-backed uacari. The only information comes from Defler (2004) who reported that day ranges for *C. m. ouakary* can vary from 50-100m to over 5km, with a mean of around 3km. Both Ayres (1986a,b), working on *C. c. calvus*, and Boubli (1997a)'s study of *C. m. melanocephalus*, found very large day ranges, with individuals travelling up to 5km per day. Boubli (1997a), working on *C. m. melanocephalus* in caatinga (a habitat with a very different pattern of productivity and annual phenology to igapó) estimated that his study troop of 70 animals ranged over an area of some 1000ha, a density of 7 animals per ha. Food availability affects daily travel distances in *C. c. calvus*, with animals travelling more widely in the period of greatest fruit abundance than in the dearth (Ayres, 1990). This is widely reported in primates and is possibly as a form of energy conservation (see Harvey & Clutton-Brock, 1981; Stevenson & Castellanos, 2000). Annual averages for day

ranges are around 2.3km per day for both *C. c. calvus* (Ayres, 1989), and *C. m. melanocephalus* (Boubli, 1997a; 1999). This is extensive for a primate of their size (Chapman et al., 2000). However, some *C. calvus* subspecies have been recorded with even longer daily ranges; Leonard & Bennett (1995; 1996) reported the average daily range for *C. c. ucayalii* to be 7.3km, and Bowler (2007) reported that the distance his study *C. c. ucayalii* travelled regularly exceeded 6km per day.

There are no data for home range in *C. m. ouakary,* though it has been calculated for *C. m. melanocephalus* (estimated minimum, 10.53km^2: Defler, 2004), and *C. c. calvus* (5.0-5.5km^2: Ayres, 1986a). The difference in extent of the ranges of two otherwise ecologically similar species may be related to the differences in productivity and phenology between the sites (Boubli, 2005). In Peru, *C. c. ucayalii* have been recorded using annual home ranges up to 30km^2, but the core area of greatest activity is much smaller – often around 2.5-3.0km^2 (Leonard & Bennett, 1996).

1.4.10 Social Ecology and Behaviour

Large group sizes, difficulties in identifying individuals, uncertainties in sexing animals, the speed with which uacaris move, their timidity and their large daily ranges have conspired to make uacaris one of the least known groups of Neotropical primates. Detailed studies of social behaviour often require conditions that permit more subtle, long-term and detailed observations than are required for dietary studies. Consequently, our knowledge of uacari society lags behind both our knowledge of uacari diets and our knowledge and understanding of the social ecology of almost all other large Neotropical primates, such as the detailed studies of Karen Strier and colleagues on *Brachyteles* (e.g. Assuncao *et al.,* 2007; Possamai *et al.,* 2007; Strier & Boubli, 2006), or of Elisabeth

Visalberghi and colleagues on *Cebus apella* (e.g. Agostini & Visalberghi, 2005; de Marco *et al.*, 2008; Padoa-Schioppa *et al.*, 2006). No previous wild studies of *C. m. ouakary* or any other uacari have yet included quantitative investigation of social ecology or social behaviour as their central theme, though Bowler (2007) devotes a chapter of his thesis to this topic. Knogge *et al*. (2006) report on a pilot project to look at the social structure of *C. c. ucayalii*, and proposed that Peruvian red uacaris have social units based on ‘’2 adult females and offspring, 2 sub-adults and one adult guarding male’’. This does not completely concord with the results of the longer term study by Bowler (20007). A recently completed field study by Bruna Bezerra (Bezerra, in prep.) on social behaviour and vocalizations of golden-backed uacaris at Jaú should provide much novel and useful information on this otherwise almost unknown aspect of uacari ecology.

Bowler (2007) provides the most detailed study so far of uacari sociology. Working on the Peruvian red uacari (*C. c. ucayalii*), he was able to confirm that groups of up to 30 with several adult males were regularly present at his Río Yavarí study site. Though bands larger than this were recorded, the wide group dispersion, so characteristic of uacaris, made it impossible to obtain accurate observations of them. This wide dispersion has other effects – Bowler (2007) reported that grooming makes up but 1.8% of the total activity budget (compared with, for example, some 9% in baboons: Williamson & Dunbar, 1999), while Barnett *et al.* (2007) reported that grooming was very rarely seen in golden-backed uacaris. Bowler (2007) reports that agonistic and display behaviours made up 41.8% of all observed social behaviours in *C. c. ucayalii*. Behaviours included penile displays, aggressive chasing, and specific behaviours (including bouncing, strutting, branch shaking and swinging from branches). These types of behaviours have been little mentioned in

other reports on this species (e.g. Aquino, 1998; Aquino & Encarnácion, 1994; Ayres, 1986a), but as social behaviour was not their focus it is hard to make valid comparisons. However, this frequency is certainly very much higher than observed for *C. m. ouakary* where social and agonistic behaviors are notably rare (Barnett *et al*. 2007a; Bezerra *et al*., 2010ab). Social behaviour is also rare in *C. m. melanocephalus* (Boubli, 1997a).

Tail wagging, where the short bobbed tail is moved rhythmically from side-to-side, is a characteristic behaviour in uacaris, having been reported whenever a *Cacajao* genus member has been studied (Barnett, 2005; Barnett & da Cunha, 1991; Boubli, 1997a; Bowler, 2007; Defler, 2004). Fernandes (1993) believed it to be a displacement activity. However, the exact function may vary between populations and species. From observations on golden-backed uacaris in Colombia, Defler (2004) suggests that this movement indicates contentment and well-being, and that its absence (accompanied by a curling of the tail between the legs like a submissive dog), is the indication of tension in the species. Meanwhile, in Brazilian populations of *C. m. ouakary*, this behavior seems indicative of tension (pers.obs.). For *C. c. ucayalii,* Bowler (2007) noted contextual differences and variations in intensity of this behaviour, and points out that *C. c. ucayalii* males have much fluffier tails than females. Together these factors, Bowler believes, may indicate that this behaviour is considerably more complex than previously thought.

1.4.11 Group Sizes

The golden-backed uacari has a fission-fusion sociality (Defler, 1999), a form of social organization also present in other uacaris species, albeit not in all populations. Boubli (1997a, 1999), for example, did not observe fission-fusion in his caatinga-living *C. m. melanocephalus* study population. In consequence, the number of uacaris reported together is generally extremely variable, with singletons, pairs and small bands being

recorded, as well as associations of 100 and even 200 individuals (Barnett, 2005; Defler, 2004). Such groupings are the largest for any New World primate (Aureli *et al*., 2008; Barnett & Brandon-Jones, 1997; Boubli, 1994). Within the genus *Cacajao* as a whole, the most commonly reported counts are of between 40 and 70 animals (Aquino 1988, 1998; Ayres, 1990; Ayres & Johns, 1987; Barnett & Brandon-Jones, 1997; Barnett *et al.*, 2005a; Bartecki & Heymann, 1987; Bennett *et al.*, 2001; Boubli, 1994, 1997a; Defler, 1991, 1999; Heymann, 1992; Mittermeier & Coimbra-Filho, 1977; Swanson-Ward & Chism, 2003). For *C. c. uacayalii*, Bowler (2003, 2007) encountered 150 individuals travelling and feeding in concert, and reported another instance where numbers may have exceeded 200. He considered that a 'group' probably consists of some 30-50 animals, with lower counts probably being sub-divisions, while the largest counts were probably aggregations of multiple groups.

For most uacari populations, the number of animals travelling and foraging together is most probably related to seasonal changes in resource availability, with the largest groups occurring at times of greatest food abundance (Aquino, 1998; Defler, 1999). However, though there were some indications of seasonal movements into mating pairs and bachelor units, uacaris on the very poor white sand caatingas (Boubli, 1997a, 1999) do not conform to this pattern, and remained in a 70-strong troop throughout the year, with no observed fissioning. In *C. calvus* (Ayres, 1989; Ayres & Johns, 1987; Bartecki & Heyman, 1987; Heymann, 1992a), and *C. m. ouakary* (Defler, 1999), large bands have been observed to fragment into smaller ones but it has yet to be determined if these have consistent composition, nor is it clear what relationship (genetic or social) exists between members of such sub-groups, nor for how long they last. Until this is established, the suggestions

that have been made by some observers, of multiple levels of social organization within uacari groups (e.g. Grüter & Zinner, 2004) must be considered speculative.

Composition of golden-backed uacari bands has yet to be reported in a quantified fashion. However, it might be expected that bands would have the same multi-male/multi-female composition as other members of the genus. Here, bands are usually composed of multiple adult males and females, sub-adults, juveniles and infants, with band membership being more-or-less evenly divided between the sexes (Aquino, 1998; Ayres, 1989; Boubli, 1997a,b). Seasonal presence of mating pairs and bachelor units have also been reported by in *C. calvus*: Ayres (1990) reported bands of up to 8 bachelor males at certain times of the year, while Bowler (2007) records batchelor groups up to 10-strong for *C. c. ucayalii*.

Irrespective of the size of a uacari band, the component members are often quite widely dispersed during travelling, with individuals separated by ten or more body lengths (>5m: Barnett, pers. obs.), which contrats strongly with the close proximity of members of most primate groups (Barnett, pers. obs.). Additionally, uacaris sub-groups often disperse widely, frequently being 1-2km from each other. Separations may last for days (Ayres, 1989, 1990; Boubli, 1999). In *C. m. melanocephalus,* Boubli (1997b, 1999) reported frequent calls which he believed facilitated within-band contact between members of a band during movement.

1.4.12 Social Structure

Little is known about the social structure of any *Cacajao* taxa. Our knowledge is an extrapolation from a few observations and disconnected incidents, and not, currently, an unambiguous analysis based on an in-depth study.

Uacari social structure is generally assumed to be peaceable and egalitarian, with the lack of strong sexual dimorphism, and infrequency of adult fighting scars and of

aggressive interactions between adults betokening a largely non-hierarchical society (Barnett, 2005). Boubli (1997a), for example, reported only one aggressive interaction between males over his entire 17-month PhD fieldwork period. The structure of uacari genitalia falls into Dixson's category of high male-male covert competition, where sperm competition is high, but physical competition is not (Dixson, 1987a,b). Males (but not females) seem to have a role in group defence, one or more remaining behind to stand between human observers, or other perceived dangers, and the retreating band. Such animals have been observed to pilo-erect, branch-shake, branch-drop, urinate, and defecate (Barnett & da Cunha, 1991; Barnett *et al.*, 2005; Barnett, pers. obs.).

Behavioural data on dominance relationships from captive uacaris are ambiguous. In a semi-captive colony in Florida, male *C. c. ucayalii* were seen to be submissive to females, who maintained a hierarchy principally through fighting (Fontaine, 1981; Fontaine & DuMond, 1977). These authors also reported that dominant females would intervene in disputes between other group members. My own general observations of a pair of caged Brazilian red uacaris (*C. c. rubicundus*), held at the Rio de Janeiro Primate Centre, showed that the male was generally dominant, driving the female away from food and water, and was markedly more aggressive towards observers. These behaviours persisted when the pair was transferred to Los Angeles Zoo and joined an existing colony of three adult females (J. McNary, pers. comm.).

Social- (as opposed to self-) grooming is infrequent in uacaris. In a free-ranging colony of captive *C. c. ucayalii*, Fontaine & DuMond (1977) observed such interactions less than a dozen times in 21 months of study. Aquino (1998) reports grooming to be rare in wild *C. c. ucayalii*, but that it was most frequently initiated by females, though in *C. m.*

ouakary Barnett *et al.* (2007) also observed grooming between male dyads. The proportion of such interactions will not assisted by the fact that uacaris generally travel, feed and rest several body lengths apart (though in the latter case younger animals may rest close together, Barnett *et al.*, 2007: *C. m. ouakary*). Large inter-individual distances also seem to be the rule in semi-captive animals studied by Fontaine & DuMond (1977).

Fontaine (1981) reported play was a common occurrence in his semi-captive *C. c. ucayalii* study group, and it occurred between adult individuals as well as between youngsters. While not reported in the wild red uacaris, extensive play bouts, often lasting many hours, have been observed between young *C. m. ouakary* (Barnett *et al*. 2007).

1.4.13 Reproduction

Observations on birth periodicity in *C. m. ouakary* are summarized by Barnett (2005), who, reviewing the few field reports available, noted that all observations of recently-born young in Brazil were clustered between Mar and Apr, the early fruiting season, that multiple males appeared to be involved in mating, and there appeared to be little aggression during the mating season. However, in Jaú, Bruna Bezerra (pers. comm.), did observe one incident of two male *C. m. ouakary* fighting, an incident violent enough to cut the face and lips of one of the participants. Defler (2004), while not reporting on mating behaviour, noted a Mar-Apr birthing periodicity in Colombia for *C. m. ouakary*, but noted a second birthing season during the late dry season (Oct-Dec). Some supportive evidence for this second peak has recently been reported from Brazil (Barnett, 2008; Barnett *et al.*, 2007). *Cacajao c. calvus* has a birth peak during Oct and Nov (dry season: Ayres, 1986a,b). Bowler (2007) observed that mating in free-ranging wild *C. c. ucayalii* occurred between late Apr and mid Jun (the drier season), and recorded infant Peruvian red uacaris

(1-3 months old) between Aug and Nov. This general reporting of clusterings of births in uacaris may indicate a narrow window of reproductive activity in the genus *Cacajao*, which would agree with Dixson's proposal (1987a,b) of brief, but intense, inter-male competition occurring in uacaris.

Based on observations of semi-captive *C. c. ucayalii* and of wild *C. m. ouakary*, the interbirth interval is estimated at roughly two years (Defler, 2004; Fontaine & DuMond, 1977). Gestation for *C. calvus* is approximately six months (Ayres, 1990). Fontaine & DuMond (1977) report that a captive female *C. c. ucayalii* was reproductively mature at 3 years old.There are no data on age on sexual maturity from the wild, though, based on observations of a captive *C. m. ouakary*, Defler (2004) suggests males may become mature at between 4 and 6 years of age. Until this age they are sexually cryptic, with testes either not descended or very small (Hershkovitz, 1993). Though cases exist of close resemblances in appearance between male and female genitalia (e.g. *Brachyteles*: Jones, 2005), for developing males to potentially conceal their sex until just before adulthood appears to be very unusual in primates (Baker & Ellis, 1994). However, in the genus *Cacajao* this also occurs in *C. c. ucayalii*, where it may be a means of avoiding aggression by adult males (Bowler, 2007).

1.4.14 Mixed Groups

The nature of inter-species associations in uacaris has received little specific attention. Their functionality has not been investigated in the same way that Smith *et al.* (2004) and Porter & Garber (2007) have, for example, for marmosets. Most of the data are simply registers of occurrences, with counts of group sizes. Even this, however, reveals some differences between taxa and also between locations. For example, while *C. m. ouakary*

on the lower Rio Negro is very rarely seen in association with other primates or with birds, studies on the lower Apaporis in Colombia found that golden-backed uacaris travel and forage simultaneously with *Lagothrix lagothricha*, *Cebus albifrons* and *Saimiri sciureus* and will feed in association with *Alouatta seniculus* (Defler, 2004). Greater anis (*Crotophaga major*: Curculidae) follow uacaris to feed on the insects disturbed by their passage (Barnett *et al*., 2005; Defler, 2004). Defler (2004) also reports that at his Colombian study site, golden-backed uacaris are regularly followed, apparently for similar reasons. by a the double-toothed kite (*Harpagus bidentatus*: Accipitridae), a small insectivorous hawk. Defler (2004) also notes that when *C. m. ouakary* feed for extended periods in one spot, the resultant fruits falling attract fish which in their turn attract pink river dolphins (*Inia geoffrensis*: Iniidae). Associations with other species have also been recorded for *C. calvus*. Bowler (2007) reported that *C. c. ucayalii* spent some 24% of the 896 contact hrs. in close proximity to one or more of all 12 of the other primate species at the study site. In total he recorded 171 associations, with the most commonly associating species being *S. sciureus* and *L. lagotricha.* Bowler (2007) does not mention associations with birds. Aquino (1988) notes associations between Peruvian red uacaris and *Cebus apella*, *Ce. albifrons* and *S. sciureus*, but not *Pithecia*. *Cacajao* and *Pithcia* have been seen associating elsewhere in Peru (Leonard & Bennett, 1996). However, though *Pithecia* is present at the Río Yavarí study site, Bowler (2007) did not record associations between the two pitheciines during his 12-month study. He posits (Bowler, 2007, p. 113) that, on the Río Yavarí, at least, such avoidance serves to minimize scramble competition.

1.5 Previous Research in Jaú

The current study took place in Jaú National Park, an area chosen for its known uacaris populations, known low levels of hunting, and the logistic convenience of proximity to a

large city (Manaus). Previous research conducted within Jaú is outlined below. A description of the park, its history, soil and vegetation types is given in Chapter 2.

1.5.1 Biological Studies

By Amazonian standards, Jaú has received a fair amount of field research. Zoologically, this has included studies of bats (Barnett *et al.*, 2006, 2007), sloths (Bezerra *et al.*, 2009), birds (e.g. Almeida *et al.*, 2008; Borges, 2003, 2004, 2006; Borges & Carvalhaes, 2000; Borges *et al*., 2004), chelonia (Rebêlo & Lugli, 1996), amphibians and terrestrial reptiles (Barnett *et al.*, 2007b; Neckel-Oliviera & Gordo, 2004), caiman (Rebêlo & Lugli, 2001), spiders (Azevedo & Smith, 2004), sphingid moths (Motta & Andreazze**,** 2001), mosquitos (Hutchins et al., 2005; Hutchings & Sallum, 2008), Hybotine flies (Ale-Rocha & Vieira, 2008), and ants (Vasconcelos *et al*., 2004).

Botanical studies have included quantification of terra firme composition (Ferreira & Prance, 1998, 1999), quantitative studies of igapó tree community composition (Ferreira & Stohlgren, 1999), and effects of inundation duration on this (Ferreira, 1997). Vincentini (2004) quantified composition of campina and campinarana plant communities and the associations between them and soil type. Castilho (2004) reported on Jaú's palms. Parolin & Worbes (2000) studied wood densities from terra firme and igapó trees. Preliminary reports on phenological data were presented by Barnett *et al.* (2008), and by Souza *et al.* (2008). The igapó communities of the adjacent Anavilhanas National Park have been quantitatively studied by Parolin *et al.* (2003a). Limnology and aquatic biology have been the subject of some initial studies (e.g. Melo *et al*., 2004).

The composition of canopy epiphytes and canopy ecology in general has yet to be studied in Jaú. There are active research programmes on giant otters (*Pteroneura*

brasiliensis), birds (including manakins), butterflies and camera-trap monitoring of terrestrial mammals. However these have yet to be published in peer-reviewed literature.

1.5.2 Human Studies

There has been considerable sociological and anthropological work at Jaú, including studies of agricultural practices (Borges *et al*., 2004), impact of these on bird communities (Borges, 2007), use of non-timber forest products (Durigan & Castilho, 2004), hunting and fishing (Pezzutí *et al.,* 2004), use and conservation of river turtles (Rebêlo & Lugli, 1996), human demography (Pinheiro & Macedo, 2004), malaria incidence (Andrade *et al*., 2005), the socio-cultural dynamics, economy and political organization of the communities within the Park (Chaves *et al.,* 2004), and the economic value of the park's existence (Santana & Mota, 2004).

1.6 Aims of the Current Study

Given the dearth of information concerning the golden-backed uacari, the remit of the present study is broad and comparatively simple: to record the diet and habitat choices over a yearly cycle of inundation, and to conduct fieldwork and in-lab observations to explain why such choices were made. Accordingly, the main aims of the study are:

- to quantify the diet of the golden-backed uacari
- to quantify plant community composition, fruit crop volume and month-by-month availability with phenological studies, in all major habitats used by the uacari within the study area
- to record habitat use and relate to resource availability
- to test the null hypothesis that the uacari eats what is available in proportion to its availability within the habitat, and, if this is not

the case, to investigate what factors influence positive and negative choice. Do this by testing aspects of physical and chemical nature of fruits, plus other modifiers.

- to use quantified behavioural sampling to record details of uacari social ecology, particularly those relating to diet, foraging formats and patterns of resource utilization
- to use data on resource use by golden-backed uacaris in Jaú to assess likely threats to their conservation within their range.

CHAPTER 2
METHODS

I know nothing except the fact of my ignorance.

Socrates

2.1 Introduction

Fieldwork was conducted under IBAMA Protected Area Study License # 138/2006, awarded in cooperation with Dr. Wilson Spironello of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, and extension CMC 008/03 of Brazilian National Research Council (CNPq) research licence ASCIN/PBC No. 157/03. Methods were developed from those used by previous uacari studies (Ayres, 1986a; Boubli, 1997a). Because neither of these authors had worked in igapó, the practicability of proposed methods was tested during visits to Jaú in Aug. 1999, Oct-Nov 2000 and Feb-May 2005. As igapó is a highly seasonal habitat (Goulding *et al*., 1988), the visits were timed to ensure coverage of the greatest possible part of the annual cycle of inundation and dry-out (Fig. II-1: Section 2.2).

2.2 Study Site

The golden-backed uacari (*Cacajao m. ouakary*) is restricted to the drainage basin of the Rio Negro in north-western South America (Hershkovitz, 1987a). It occurs in the Amazonian portion of both Brazil and Colombia, with the majority of this primate's range lying in Brazil (Barnett, 2005 and Fig. I-1). Though uacaris occur in non-protected areas within this vast area, it was decided to work in an existing protected area since: a) animals might be hunted less and therefore be more approachable, and b) a habituated band would then be less likely to be hunted after the end of the study.

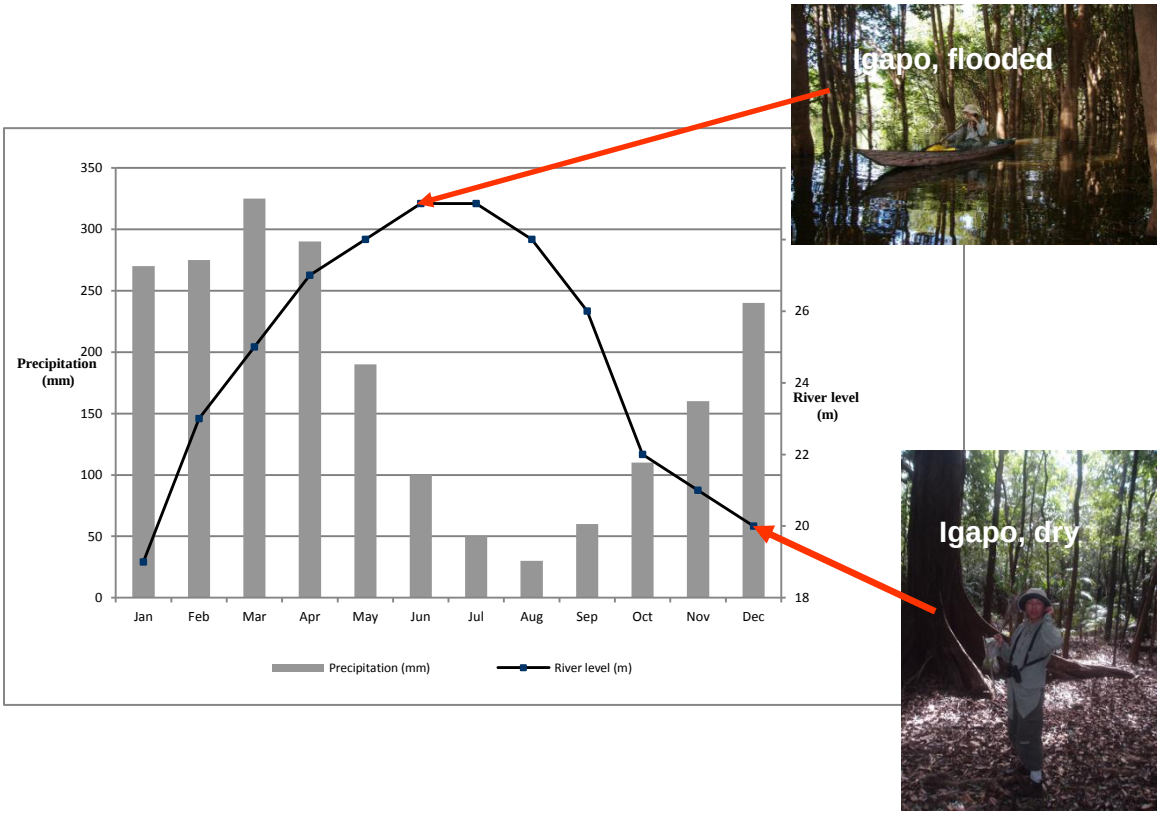
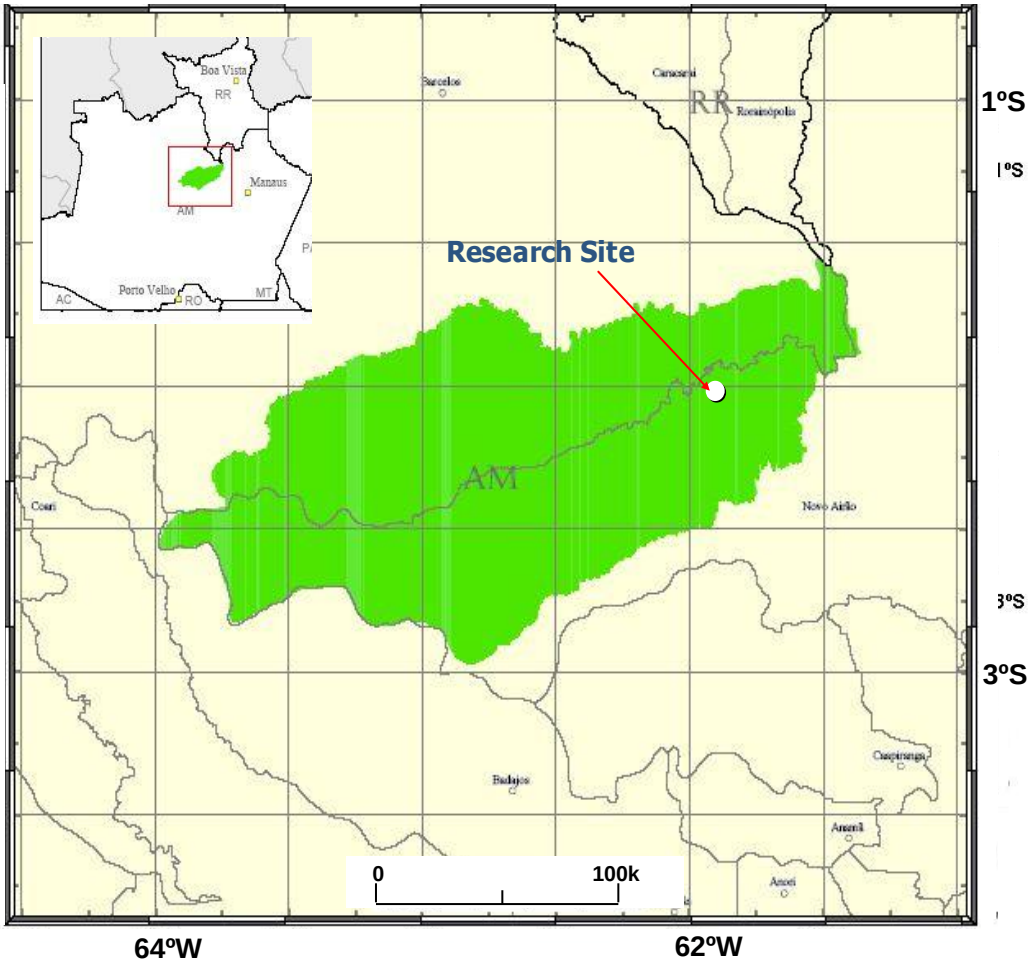


Fig. II-1: Monthly Variation of Rainfall and Riverwater Levels in Central Amazonia

2.2.1 Locality

Field studies were conducted in the Parque Nacional do Jaú (PNJ), a 2,369,000ha area on the southern bank of the Rio Negro, some 220km west of the city of Manaus in the Brazilian state of Amazonas (1°40'-3°00'S and 61°26'- 64°00'W: Fig. II-2). PNJ was established as a fully protected area in 1980, being designated as a National Park by Federal Decree No. 85,200, and received its first Management Plan in 1997. In 2001 it was designated part of UNESCO's Central Amazon Biosphere Reserve. PNJ is administered by IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renovaveis), the Brazilian natural resources agency, and by Fundação Vitória Amazônica (FVA), a Manaus-based conservation not-for-profit organization.

PNJ embraces the entire 1,000,000ha watershed of the Rio Jaú, a 300km-long blackwater river which traverses the park south-to-north through its geometric centre (Fig. II-2). The mouth of the Rio Jaú is at 61°25'.11''W, 1°51'41''S.



Source: Brazilian Environment Ministry, 2005

Fig. II-2: Map of Jaú National Park, Showing Research Site

Along its length, the Jaú has some 1500 recognised affluents. Together, these tributaries have a total estimated length of some about 5700km. The eastern boundary of the park is formed by the Rio Carabinani and the western by the rios Unini and Paunini, its major affluent. PNJ has two major habitats, terra firma and igapó (see below) and a

number of minor habitats that include palm swamps (buritízal), aroid swamps (aningal), campina (white sand scrub), campinarana (species-poor forest on white sand) and some cloud forest on tall hills. Together, these five minor habitats constitute some 26% (711,275ha) of the park, with terra firme constituting 63% (1,710,850ha) and igapó some 297,875ha (11%: all values calculated from data in Pinheiro & Borges, 2004). The human population, spread across some eight small villages, with other families living solitarily or in small communities, totals around 1000 adults (a density of some 0.3 people per ha). In 2002, FVA reported 41 families living on the Rio Jaú and 4 more living along the Carabinani. The same survey also recorded 138 families living along the Rio Unini, though many were living outside the reserve. There has been no great influx of people into the Park since this 2002 survey (S. Borges, pers. comm.). The human density in PNJ is some 14% the average for the Brazilian Amazon (2.1 individuals per ha - Instituto Brasileiro de Geografia e Estatística, 2007), and only 7.5% of the average for the entire basin of 4 people per ha (Perz *et al*., 2005).

Originally an isolated protected area, Jaú more recently became part of a trans-interfluvial conservation area that is linked to the with the 1,124,000ha Mamirauá Sustainable Development Reserve (Masterson, 1996), *via* the 2,350,000ha Amanã Sustainable Development Reserve (established 1997: Amaral *et al*., 2005; Anon., 1998) and the 830,000ha Unini Extractive Reserve (established 2006: Salisbury & Schmink, 2007). Together they form a contiguous protected area that exceeds 6,576,000ha, an area larger than either Switzerland or Sri Lanka, and nearly the size of Ireland. Collectively known as the Central Amazonian Conservation Complex by UNESCO, these units combined form the planet's largest protected tropical forest. Of this, some 5,452,000ha

(an area more than half the size of Portugal) is blackwater ecosystem, and therefore (at least potentially) habitat for the golden-backed uacari.

Hunting currently occurs at limited levels in Jaú, with subsistence take of agoutis (*Dasyprocta agouti*: Dasyproctidae), paca (*Agouti paca*: Cuniculidae), deer (*Odocoileus virginianus*: Cervidae), tapir (*Tapirus terrestris*: Tapiridae - Fleck & Bodmer, 2005; Pezutti *et al*., 2004). Use of forest resources is restricted to subsistence removal of fruits (such as buritĺ, *Mauritia flexuosa* and açaí, *Euterpe oleracea* - both Arecaceae), vines (e.g. ambé, *Heteropsis* spp.: Araceae), and barks for manufacture of artesanal products (e.g arumã, *Ischnosiphon polyphyllus*: Marantaceae: Durigan & Castilho, 2004). Though poaching occurs, it is primarily restricted to river turtles and various fish. Such illegal operators are unlikely to kill monkeys while working because of the revealing noise firearms would make (blow-darts are regional archaicisms). However, the fauna and flora in the region is not pristine as the area was heavily exploited between the 1880's and 1960's for timber, rubber, meat and skins; during this time the city of Velho Airão (now in ruins) was a major trading point on the lower Negro and fuelled a substantial commercial trade in natural products (Galvão, 1959 and Leonardi, 1999 give descriptions of the historical life and times of the region). The impacts were such that the larger mammals suffered severe loss of numbers, with giant otter and other fur-bearing species being severely reduced. Among the primates, this probably includes such large species as *Ateles paniscus* and *Lagothrix lagotricha* (Barnett *et al*., 2005a), though probably not *Cacajao m. ouakary*, as this is not a species that generally attracts much hunting interest (Barnett, 2005). Agriculture in PNJ is of a subsistence nature and revolves around the cultivation of manioc (*Manihot esculenta*: Euphorbiaceae) in small fields, in which a few

supplementary items (such as cará, *Dioscorea* sp.: Dioscoreaceae, and banana, *Musa paradisica*: Muscaceae, plus some 17 others) are also cultivated (Borges *et al*., 2004a). Worked on a 5-year rotation, these clearings are generally small and are not considered to have impacted the forests of Jaú greatly (Borges *et al*., 2004a). Within 15 years, secondary forest to a height of 10m with as many as 37 tree species per 0.5ha can have re-established naturally (Eliana Andrade and Eduardo Souza, pers. comms.).

2.2.2 Climate

The climate of PNJ is typical of that of the Amazon basin, in that its seasons are defined by rainfall and riverine flooding (Fig. II-1). Flooding is highest during Jun and Jul when lakes can flood between 5.7-10.5m. Average rainfall differs between months, being 1750mm between Jul and Sep, and 2500mm between Dec and Apr. In May-Jun and Oct-Nov there is usually very little rain (Fig. II-1). Annual average temperature ranges from 26ºC to 26.7ºC. At Jaú, the highest-ever recorded temperature was 37.7ºC, and the lowest 22ºC (Pinheiro, 1999). Higher temperatures are recorded as rainfall and water levels fall, and lower ones when water levels and rainfall are highest. The rivers and streams are blackwater, with a low biomass but high species diversity. The pH levels are lowest during the dry season in late autumn and may reach 2.7, an acidity value near the physiological limit for many types of aquatic organisms (e.g. Gonzalez & Dundon, 1989).

2.2.3 Geology and Soils

The Jaú river basin is composed of five different geological formations (Pinheiro & Borges, 2004). The Solimões Formation dominates, occupying some 65% of PNJ. The Park's three major rivers, the Unini-Pauini, the Jaú and the Carabinani, are all boundaried by Holocene Alluvial Deposits. The remaining three formations (the Prosperança,

Trombetas, and Barreiras) are all confined to the north of the park (Fig. II-3). Of these, the Prosperança Formation and the Holocene Alluvial Deposits occur in the study area (the red rectangle in Fig. II-3).

Prosperança Formation: In the south of the Park these Precambian sedimentary rocks (570-510 million ybp) are overlain by the 5.6-1.6 million year old lacustrine deposits of the Solimões Formation, the remnants of a large Amazon lake (Frailey *et al*., 1988). Here soils are moderately fertile (by the low standards of Amazonia: Laurance *et al.*, 1999, 2001). But the soils of the northern quarter (in which the study was undertaken) are derived directly from these much older poorer substrates and are therefore often sandy, quick-draining and nutrient poor.

Holocene Alluvial Deposits: Some 10,000 years old and occupying around 7% of PNJ, it is these soils on which igapó forests grow. These deposits are characterized by a clay-like nature, the result of fine sediment deposited when, in response to climatic changes associated with deglaciation, the Rio Negro river system carried abundant suspended load. The finer portions of these sediments were trapped by coarse sands that had been already deposited during earlier geological cycles (Latrubesse & Franzinelli, 2005). The differential rates of erosion and deposition during the alternating wet and dry periods of the Holocene (Latrubesse & Franzinelli, 2002; Steveaux,

2000), have thus provided the current system of river terraces and banks that limit the physical distribution of igapó vegetation.

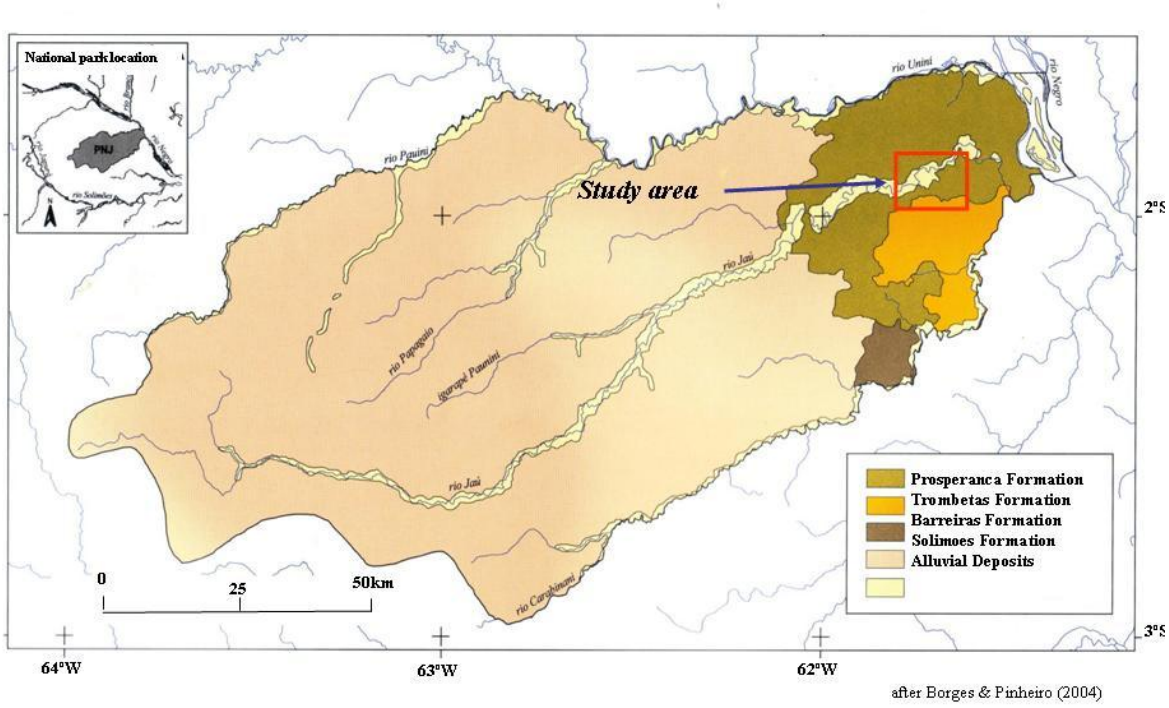


Fig. II-3: Geology of Jaú National Park

2.2.4 Habitat Types

The two dominant habitat types in Jaú are terra firme and igapó forest types. There are also minor forest types: aningal, borokotò, butitizal, campina, campinarana and montane forest. The composition of these habitat types is considered below. Photographs of the four major habitats visited during the current study are given in Fig. II-4. Regenerating farmland covers a minimal area, as do such features as sandbanks and beach vegetation.

Igapó

Terra firme

Borokotò

Capoeira

Fig. II-4: Habitats Sampled with Quadrats

Terra firme: inventories at Jaú have found between 137 and 168 tree species per ha (Ferreira & Prance, 1998). This is similar to the 179 tree species of 15cm dbh or more recorded in a 1ha plot near Manaus by Prance *et al*. (1976). Studies by Vincentini (2004) ranked the following five species highest in Importance Indices: *Eschweilera bracteosa* (Lecythidaceae), *Protium grandifolium* (Burseraceae), *Alexa* sp. (Fab.: Pap.), *Tachigalia venusa* (Fab.: Caes.), and *Swartzia polyphylla* (Fab.:Pap. = *S. acuminata*).

Igapó: The Amazon basin is unusual amongst tropical river systems in the extent of the flooded forests that border its rivers (Goulding, 1990; Parolin *et al*., 2004a,b). Prance (1979) distinguished two kinds of flooded forest: that which occurs on the margins of silt-rich white-water

rivers, known as várzea and that which occurs on the margins of silt-poor black-water rivers, which are called igapó. Sedimentological analysis of the Amazon Basin's lacustrine-riverine history suggests that várzea forests are much younger than igapó forests; the latter having been in existence since the Late Cretaceous, 100-65 million years bp (Mybp), whilst the former developed only after an Andean orogeny some 25 Mybp caused the Atlantic drainage of the Amazonas graben to form the Amazon River (Clapperton, 1993; Kubitski, 1989). The current river systems of northern South America did not begin to establish until 90 Mybp, with the present white-water hydrogeography becoming established less than 20 Mybp (Mertes *et al.*, 1996).

These two kinds of flooded forest differ greatly in the extent and topography of their floodplains. Nile-like, those of várzea are formed by the deposition of silt and so are both horizontally extensive (often to several km), and formed by a complex (and diversity-enhancing) system of sloughs and leveés (Ayres, 1986a), that resembles an extensive ridged blanket of vegetation. In the absence of silt, igapó lacks a slough-and-leveé system. The floodplains of blackwater systems are therefore, in contrast, more of a marginal ribbons of vegetation, and these rarely exceed 200m in width (though more extensive areas may form in the margins of lake and other shallow areas). In Amazonian terms, igapó is a species-poor habitat (Parolin, 2003; Parolin *et al*., 2003a, 2004a). For example, Haugaasen & Peres (2006) recorded 99 tree species from 3

one-hectare plots in igapó, but recorded 150 tree species in várzea and 255 in terra firme.

There is however, great spatial heterogeneity within igapó due to varying degrees to which its component tree species tolerate inundation (e.g. Parolin, 2001a,b, 2002a,b for seedlings; Parolin *et al*., 2000b for adults). The floodplain of blackwater rivers is narrow but steep, which as one moves further from the shore, can lead to great variation in the length of time areas are inundated, with substantial differences being possible over short dirtances (Ferreira, 1997; Parolin *et al*., 2000b). Combined these factors lead to strong horizontal banding in the distribution of igapó tree species (Ferreira, 1997, 2000; Parolin *et al*., 2004a), with the width of the bands being determined by the local topography of the river margin (Parolin *et al*., 2005).

Specializations in physiology, phenology, growth strategies, leaf size & shape, seed germination strategies, and fruit anatomy (Ferreira, 2002; Kubitzki & Zibursky, 1994; Parolin, 1998, 2000a, 2001a,b, 2002a,b; Parolin *et al*., 2001, 2003b), mean that there are frequently tree sister species in terra firma and igapó (e.g. Gottsberger, 1978; Parolin *et al.*, 2004b). A high percentage of igapó fruits are dispersed either by water (hydrochory) or fish (ichthyochory: Gottsberger, 1978; Kubitzki & Zibursky, 1994). The consequent requirement for synchronization with the pulsing of river water levels results in a broad coincidence of fruiting maturation across the igapó tree community (Ferreira, 2002; Ferreira &

Parolin, 2007). Species characteristic of igapó include *Eschweilera tenuifolia* (Lecythidaceae), *Amanoa oblongifolia, Hevea brasiliensis* and *Mabea nitida* (all Euphorbiaceae), *Macrolobium acaciifolium* (Fab. Caes.), *Tabebuia serratifolia* (Bignoniaceae) and *Buchenavia orchrogramma* (Combretaceae).

Because of low nutrient supplies and cambial dormancy during the peak of inundation (when many species shed their leaves), igapó trees generally grow very slowly. For example, dendrochronological records give a mean radial increment (MRI) of 1.52±0.38mm per year for adult *Macrolobium acaciifolium* trees (Schöngart *et al.*, 2005), and many of the analysed trees were over 500 years old.

Aningal: a permanently flooded habitat dominated by the aborescent herb, *Montrichardia aborescens* (Araceae), a semi-woody aroid whose wrist-thick stems may reach 3m in height. Jaú's aningais have yet to receive quantitative botanical studies, but a study of an aningal in Venezuela (Gordon & van de Walk, 2003) found 53 species of flowering plants. Besides *M. arborescens*, other common species were the shrub *Hamelia patens* (Rubiaceae), and the vines *Mikania cordifolia* (Asteraceae), *Sarcostemma clausum* (Asclepiadaceae) and *Vitis caribaea* (Vitaceae: Gordon & van der Walk, 2003). In Jaú's ainigais, trees, even woody shrubs, appear rare (Barnett, pers. obs.).

Borokotò: the steepness of the river bed in black-water rivers, the absence of a floodplain and the consequent physiological division of tree-species into flood-tolerant/flood-intolerant, means that the ecotone between igapó and terra firme is generally a very narrow one. Borokotò, however, is the one habitat where the plants of the two habitats can be found together. This is because of the presence there of mounds to 7m tall and over 20m in length, which provide dry land even when the forest is flooded. As a result, the flora contains both igapó and terra firme elements (Barnett *et al*., 2007). This very interesting habitat does not seem to have been formally studied before.

Butitizal (pl. buritízais): these are permanently swampy areas, with hummocks of slightly higher ground that will be exposed in the low water season. A low alpha-diversity forest type, they are dominated by burutí palms (*Mauritia flexuosa*). In some areas this palm may form mono-dominant stands, though a low diversity mixed plant community is more common. Even then, burutí always dominates. Understory is generally poorly developed, and lianas rare (Kalliola *et al*., 1991). These swamp forests generally occur in narrow depressions paralleling river beds, where the substratum is clayey and so retains rainfall (Kahn, 1991). The soil is characterized by an accumulation of slightly decomposed organic matter (mostly shed fronds, inflorescences and infrutescences of *M. flexuosa*). Palm density may be very high, reaching some 130-250 adult plants per ha (which exceeds the density of palm oil

plantations: Kahn, 1988). Buritĺ fruits have a thick soft pericarp that is eaten by a great diversity of birds and mammals (Bodmer, 1990; Fragoso & Huffman, 2000; Renton, 2002; Storti, 1993).

Campina: the white sand soil on which campina grows (Rebelo & Williamson, 1996), is both nutrient-impoverished and unable to retain water (Anderson, 1981). Ground cover includes the insectivorous plants *Drosera* (Droseraceae), and *Pinguicula* and *Ultricularia* (both Lentibulariaceae). Open areas of sand are often covered by mats of a blue-green alga (*Stigonema tomentosum*: Stigometomaceae). There is often a local abundance of lichens and mosses on living branches and the soil surface, and the ground may be covered with a spongy mat of *Cladonia* lichen or tussocks of *Paepalanthus fasiculatus* (Eriocaulaceae). Sphagnum is infrequent (Pires & Prance 1985; Prance 1987, 1989). Rarely more than 2m tall, the woody vegetation is essentially scrubby and shrubby, and has a very open and broken canopy. Component species have many xerophytic adaptations, including thick bark and small, tough, shiny leaves. At PNJ, the woody cover is dominated by *Humiria wurdackii* (Humiriaceae), *Ilex costata* (Aquifoliacae), *Bactris campestis* (Arecaceae), *Doliocarpus areolatus* (Dillenaceae) and *Lacmella macrocarpa* (Apocynaceae: Vicentini, 2004). A high proportion of the fruit from the 58-species strong woody plant community (Vincentini, 2004) are small and berry like.

Campinarana: species-poor forest, characterized by high densities of thin-trunked species, and divisible into two sub-classes, low campinerana (height of canopy 6.2±1.9m), and tall campinerana (height of canopy 9.5±1.2m: Vincentini, 2004). Including palms, there some 55-60 woody species in each sub-habitat. Based on Importance Indices calculated by Vincentini (2004), the five main species in Jaú's low campinerana are *Pradosia schomburgkiana* (Sapotaceae), *Macrolobium caniculatum* (Fab.: Caes.), *Dimorphandra vernicosa* (Fab.: Caes.), *Gongylolepsis martiana* (Asteraceae), *Protium heptaphyllum* (Burseraceae) and the five main species in high campinerana are *Macrolobium caniculatum* (Fab.: Caes.), *Iryantheira elliptica* (Myristicaceae), *Ecclinusa* sp. (Sapotaceae), *Brosimum utile* (Moraceae) and *Hevea* sp. (Euphorbiacae).

Montane forest: the area of montane forest in PNJ is very small, and occurs on hills reaching 600m in altitude. The habitat has yet to be studied (Pinheiro & Borges, 2004; S. Borges, pers. comm., 2007).

2.3 Fieldwork Sites

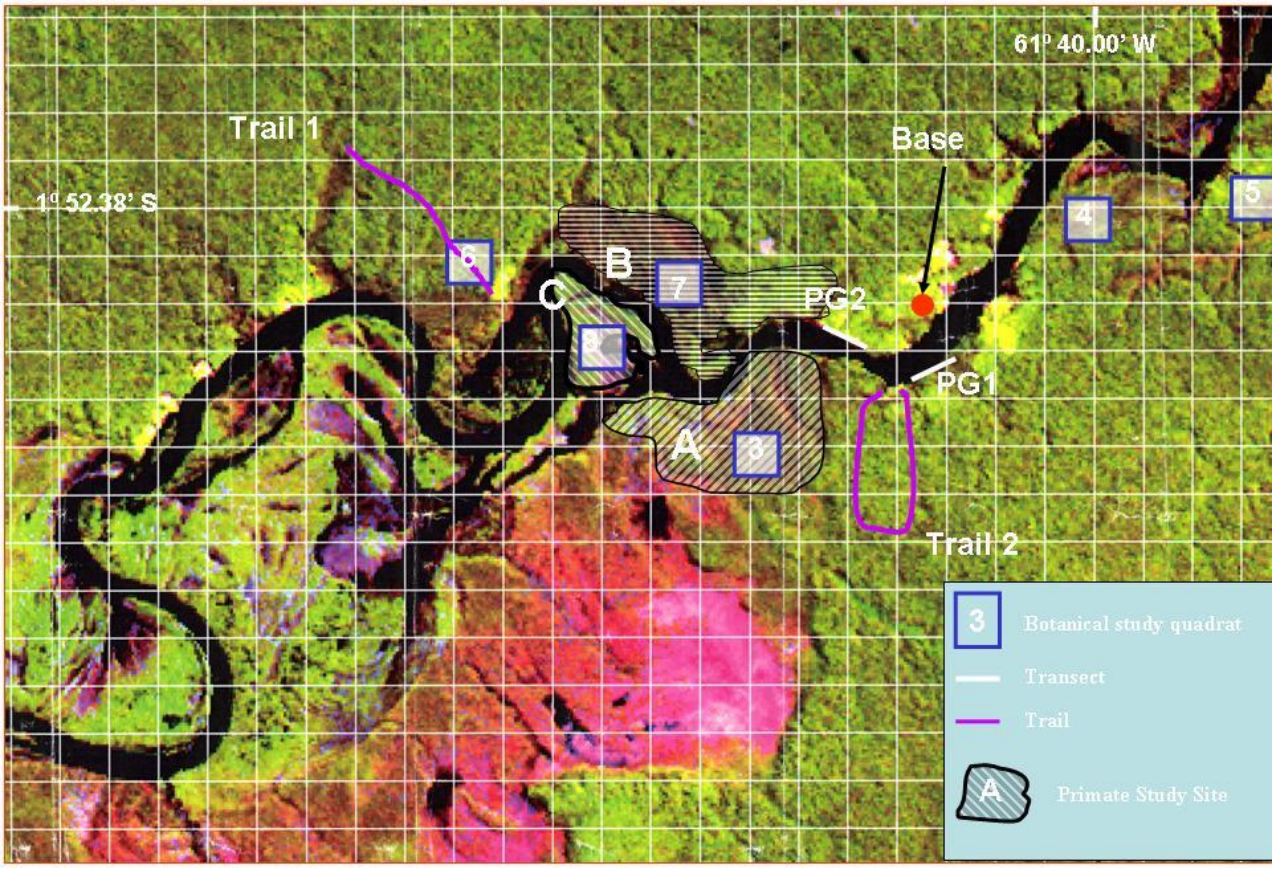
Work was carried out in forests within 4km of the research base. Located at 01º 53.568''S, 61º 41.482''W, this is the former site of the FVA-IBAMA floating research station, from which preliminary work on the uacaris was conducted in 2000 and 2005 (Barnett *et al.,* 2005a,b,c, 2006, 2007). The research area lies approximately mid-way between the Cachoeira do Jaú ('Jaú Rapids', 01 º 53.21"S, 61 º 40.43"W), and the village

of Patuá (01º 53.16”S, 61º 44.31”W). The fauna and flora of the study area are subject to subsistence use by local inhabitants, but hunting is minimal and extraction of timber and other forest products is restricted to a subsistence basis (it is also prohibited in the Park management plan: Pezzuti *et al.*, 2004; Pinheiro & Borges, 2004). Three areas of igapó were investigated. Fieldwork began in Oct 2006 and ended in Apr 2008, with field work occurring in 15 of these 19 months. Positions of all quadrats, primate study sites, transects and trails are shown in Fig. II-5 (each grid square is 0.5km^2).

2.4 Fieldwork Structure

2.4.1 Introduction

Almost every field-based question in primatology has a number of alternative methodological solutions (Setchell & Curtis, 2003), differing subtly in rationale and implementation. In this section I provide explanations and rationales for the methodologies I chose as they relate to work on a timid little-known fast-moving animal in the canopy of a largely unstudied and under-reported tropical habitat.



Source of original satellite map: Brazilian Space Agency *via* Fundação Vítoria Amazônia.

Fig. II-5: Research Site showing Trails, Quadrat Locations and Primate Study Zones

2.4.2 Botanical Composition and Phenology

To provide a quantitative basis for diet comparisons (James & Shugart, 1970), the species' composition of the various forest types was analysed, using quantitative quadrat-based community sampling and phenological studies (Section 2.6). Golden-backed uacaris have not been recorded in campina, but are known to use borokotò, capoeira and terra firme (never-flooded) and flooded forest types (igapó: Barnett *et al*., 2002, 2005a, 2007, 2008). It is common for these habitats, even when adjacent, to have asynchronous phenophases (Haugaasen & Peres, 2005ab, 2007a). To assess the potential food resources available to uacaris effectively, and then analyse the use they made of them accurately, it

was vital to know not only the sequence of availability, but also its extent. The latter was important because in the igapó not all conspecific trees may flower at the same time (Parolin *et al*., 2002), and it is not uncommon for tropical tree species to have supra-annual reproductive cycles (Bawa *et al.*, 2003). However, a number of previous studies (e.g. Maia & Piedade, 2000, 2002a, for *Eschweilera tenuifolia*; Maia & Piedade, 2002b, for *Hevea spruceana*), have recorded only whether a species was, or was not, flowering or fruiting in a particular month – the absence of data on the amount of available resources severely hampers studies seeking to understand the basis for diet choice in a particular species of animal.

For phenological studies (sections 2.6.2, 2.6.3), it was important to obtain data on all species in the study area. However, comparing lists of collected plants from the region with quadrat species lists showed that quadrats did not contain all plant species present in the study area. In addition to this lack of representativeness in terms of species, there is the problem of lack of representation in terms of activity. This is problematic because, while it is common for rainforest species to have highly synchronous phenologies (Adler & Keilpinski, 2000; Poulin *et al*., 1999), there is some intraspecific asynchrony (Franklin & Bach, 2006). This can be especially marked in species, like many in igapó (Parolin *et al*., 2002a,b), where the lengths of fruiting or flowering seasons may be extensive (up to 8 months), and where duration of the species' fruiting phenophase may exceed that of an individual plants'. Therefore, it is not certain that the phenological activity of the individual trees in a quadrat is indicative of the phenological activity of the species as a whole. In extreme cases, adult individuals of the same species may not even flower in the same year (e.g. Cannon *et al*., 2007). Consequently, in the igapó areas under study not all

individuals of a species might be in flower, fruit or the same leaf phenophase at the same time. It was therefore possible that individuals of a species represented in a quadrat might be in flower or fruit elsewhere in the forest but not in the quadrat. This problem of representativness becomes acute because uacaris range so widely. These considerations have prompted other workers (often also working with widely-ranging species) to supplement quadrat based phenologies with transect-based studies in which fruits and flowers that have fallen to the ground are noted and the species identified (van Schaik & van Noordwijk, 1985; Wich & van Schaik, 2000). This approach was adopted in this study and the methods are discussed in Section 2.6.3.

2.4.3 Crop Volume

Just as simply recording the phenophase in a 'present-absent' manner can obscure the subtleties of primate diet choice, so it is helpful to have numerical estimates of crop volume. This can help explain times spent in individual canopies as well as the presence or absence of species in the diet of a primate (Section 2.13). When considering crop volumes it is important to remember that the biomass (that is, number *x* weight) of fruit borne by trees varies substantially both between species, and between individuals of a single species (Singh & Kushwaha, 2006). This, combined with variation in the size of the canopy of individual trees, contributes to variation in patch size; a variable in optimal foraging that has been shown to be important in influencing primate diet item choice (Irwin, 2007; Phillips, 1995; Wallace, 2008a,b).

2.4.4 Food Choice Cues

A diversity of cues and properties of fruits and other diet items have been shown to influence the choice of an item as part of the diet of individual primates (Gautier-Hion *et*

al., 1985; Julliot, 1996; Kinzey & Norconk, 1990). Consequently, I attempted to include all measurable and analysable variables likely to be influential in diet item choice. Apart from responding to absolute abundance of fruits (Cunningham & Janson, 2006; Stevenson, 2004: an aspect tested by quantitative botany in Section 2.7.1), a number of other characteristics have been recorded as influencial, including: fruit size (Kunz & Linsenmair, 2007, 2008a), hardness (Kinzey & Norconk, 1990; Oftedal, 1991), colour (Julliot, 1996; Urbani, 2002), and the irritant hairs (Tutin *et al*., 1996), spines and resins that increase handling time (Hemingway, 1996, and review by Garber & Lambert, 1999). The presence of noxious secondary compounds (Glander, 1982; Stevenson, 2004), both as toxins (review, Lambert & Kaplin, 2001), and anti-feedants (Wrangham *et al*., 1998) can also influence diet choice, though these data must be interpreted cautiously (Janzen, 1978), as trade-offs frequently exist (*viz* Norconk & Conklin-Brittain, 2004). Maturity stage is also often very important (Brockman & van Schaik, 2005; Kunz & Linsenmair, 2007; Poulsen *et al*., 2002).

Descriptions of the physical properties of fruits have been widely used in primate diet studies (e.g. Gautier-Hion *et al.*, 1985; Happel, 1986; Lapenta *et al*., 2003; Sourd & Gautier-Hion, 1986: also Section 2.9). To try and understand what parameters are being used in diet item choice, it is important to consider the perceptual physiology and sensory physiology of the primate species involved (Dominy *et al*., 2001).

2.4.5 How Foods Processed

It is important not only to consider what fruits are eaten, but how they are eaten. Though the energetic cost of a single bite may not be great, the cumulative effect of its repeated action over the course of a day, season and lifetime makes it highly likely that animals will attempt to minimize force expended when biting (e.g. Dumont, 2007; Ross *et al*.,

2007). In addition, teeth damaged by the application of inappropriate or excessive force are not only less effecient, but also more prone to abcesses and other infections, which in wild individuals of a number of different mammals species have been shown to be potentially life-threatening (Patterson *et al*., 2003). Hence, one might expect the application of bite force to be optimized. Fruit pericarps often vary more in thickness than can be expained by simple allometry, providing an opportunity for fruit selection by animals that would access the seeds, including uacaris (Toju, 2008; Toju & Sota, 2006). In addition, especially in dehiscent fruits (Section 2.9.6), penetrability is not always uniform across the pericarp surface.

2.4.6 Quantifying Selectivity

Choice ratios express the selectivity of a primate in relation to the availability of resources. The proportion of an item in the diet of a primate very rarely maps 1:1 onto the proportional availability in the primate's habitat. Though cultural factors (Boesch *et al*., 2006), and age-cohort (MacKinnon, 2006: Robl, 2008) may be influential, the difference between availability and use is generally attributed to active choice by the primates of one food item over another (e.g. Fragaszy & Boinski, 1995; Marsh, 1981), with the inherent assumption that estimates of nutritional quality are the key deciding factors (e.g. Dew, 2005; Li *et al*., 2003; Zhou *et al*., 2006). As nutritional data was not available, choice ratios were tabulated considering only the availability-based variables.

2.4.7 Fieldwork Parts

The study was divided up between the following activities:

> *Part 1:* (Oct 2006-Feb 2007): habituation of uacaris in three locations, setting up of botanical quadrats and start of plant identification program and collection of phenological data.

Part 2: (Mar 2007-Apr 2008): quantified studies, including - collection of feeding and time-budget data from uacaris, physical characteristics of diet items, crop volumes, faunivory, characteristics of feeding trees, measurement of nectar sugar concentrations of eaten and non-eaten flowers.

This was followed by a laboratory-based period: *Part 3*: (Jun to Dec 2008): chemical analysis of eaten and non-eaten plant material.

Methodologies will be described in the order given above. Data were collected for a total of 238 days (73 in Part 1, and 165 in Part 2). Gaps in data collection occurred due to bad weather, ill health or family bereavement. A number of people assisted me with the fieldwork. Their responsibilities and periods of participation are given in Table II-1.

Table II-1: Fieldwork Personnel for Current Study

Person	***Responsibility***	***Period Active***
Thais Almeida	Assistant field biologist: diets of parrots and non-uacari primates. Recording primate activity in non-flooded forests.	Oct 2007 – Oct 2008
Eliana Andrade	Assisted with habituation studies, setting up quadrats, initial data collection. Organized timber data collection from sawmills, and home base logistics.	Oct 2006 – Apr 2008
Bruna Bezerra	Had own project (*ver* Bezerra, 2010), but provided assistance with habituation and setting up quadrats. Later, provided *ad hoc* assistance with food item specimen collection & uacari fæcal samples, and with observations of interest to current study.	Nov. – Dec. 2006 May-Aug. 2007
Roberto Morrera*	Guide and field assistant: Uacari location and orientation within forest. Boatman, principle tree-climber, provider of local plant names and local biological lore.	Oct. 2006 – Oct. 2008
Eduardo de Souza*	Guide and field assistant: Uacari location and orientation within forest. Principle boatman, tree-climber, provider of local plant names and local biological lore.	Oct. 2006 – Feb. 2009
Welma Souza Silva	Assistant field biologist: collection of phenological data, finalizing botanical indentifications, assisted with crop-volume data collection	Nov. 2007 – Feb2009
Jefferson Valsko	Assistant to Thais Almeida	Nov. 2008

***Note:** other local men worked as short-term field hands as-and-when the project required, principally assisting with cutting or maintaining trails and collection of botanical specimens. Welma Souza Silva also contracted Amazonian parataxonomist Sebastião Salvino de Souza ('Saba') to visit the quadrats and double-check her tree identifications.

2.5 Habituation

Studies in 1999, 2000, and 2005 had provided a total of some 53.5 contact hrs. across 52 field days in Aug. 1999, Oct.-Nov. 2000, and Mar.-May 2005 in both wet (unflooded) and dry (flooded) seasons (Barnett *et al*., 2005a,b,c: Fig. II-1). These field experiences had indicated that golden-backed uacaris were timid animals, who rarely permitted observers closer than 20-30m before flight ensued. This behaviour was in marked contrast to that of other species of primate in Jaú; when groups of *Alouatta seniculus, Cebus albifrons, Ce. apella* and *Saimiri sciureus* were encountered in the field, all permitted observers to within 10m for prolonged periods early on in the fieldstudy even before repeated contacts. Consequently primate studies during Oct. 2006-Feb. 2007 (Part 1) was devoted to habituating the uacaris, trying to get progressively closer and simply following them at a distance whenever they took flight. Habituation was complicated by the fact that bands appeared to have overlapping ranges and that the fission-fusion nature of uacari society meant that, over the weeks of habituation, while some animals had doubtless seen us before, but others had not and reacted with alarm. Given these circumstances, three areas were visited for 73 days in the 5 months of the habituation period (Oct, Nov, Dec 2006, Jan, Feb, 2007). These areas are marked *A, B,* C on Fig. II-5. After five months the animals in these three areas generally permitted us to within 10m, allowing good quantified observational data to be obtained using binoculars. This period also allowed testing of the observational field methods and familiarization with the behavioral repertoire of the uacaris. Detailed fieldwork on uacaris began in Mar 2007 and continued until Apr 2008. Data collection on parrots and other primates continued until Oct 2008, and for plant phenologies continued until Jan 2009.

2.6 Quantitative Botany

To provide a quantitative basis for diet comparisons (James & Shugart, 1970), the species composition of the various forest types was analysed. Data concerning when fruit and flowers became available, and in what quantity, came from phenological studies, using quadrats, study transects and 'pheno-trails' through the igapó. The vascular epiphyte communities of igapó and terra firme were not quantified.

2.6.1 Quadrats and Transects

Quadrats of 0.25ha (125x20m) in area were located in all habitat types from which uacaris had been recorded in previous study visits. Photographs of the habitat types appear in Fig II-4. Quadrats were placed in: igapó, borokotò (hummock igapó), capoeira (secondary forest) and terra firme (never flooded evergreen lowland rainforest). Details of the quadrat placements are provided in Table II-2, their geographical positioning and distribution is shown on Fig. II-5. Geographical coordinates given in Appendix II-3. Each quadrat was centered on a tree in which uacaris had been seen feeding during the habituation period. As with many seasonally-flooded habitats (e.g. Capon, 2005), igapó shows distinct communities whose composition is related to the tolerance of the component plant species to inundation (Ferreira, 1997; Ferreira & Stohlgren, 1999; Section 2.2.4). Because of this, three 0.25ha quadrats were placed in different parts of the igapó forest, with quadrats 3, 7 and 8 being progressively closer to the interface of the forest edge and the river. In addition, two quadrats (PG 1 and 2) were placed at the very border of the igapó with the river in order to sample the very different flora there. This river margin community is very distinct, but very narrow. Each PG quadrat was 250m long and 5m wide. They were deliberately shaped to be long and narrow so as to provide

an adequate sample a very spatially-restricted habitat. and ensure that only edge vegetation was sampled. The data from these two thin quadrats (their combined area equaling 0.25ha) was pooled. This was done to capture a distinct forest edge community which had not been included in the other igapó quadrats and whose botanical composition would otherwise have remained unrepresented in the data sample.

Table II-2: Botanical Quadrat Habitat Placements

Quandratnumber*	***Habitat type***
3	igapó
4	borokotò
5	capoeira
6	terra firme
7	igapó
8	igapó
PG 1	igapó margin
PG 2	igapó margin

* ***Note***: 1 and 2 were small method-testing quadrats set up in 2005 and were not used during the current study.

The four sampled habitats represent all the major habitat types in the area. The uacaris at Jaú were recorded using neither campina (a very open habitat of low scrubby bushes and trees, *ver* Section 2.2.4), nor aningal (a habitat of shallow swamps near-monodominant for *Montrichardia aborescens* [Araceae], *ver* Section 2.2.4). Both these habitats were therefore excluded from the study. Buritízais, the seasonally flooded palm stands dominated by the burití palm *Mauritia flexuosa* (*ver* Section 2.2.4) were excluded because none were within practical reach of the study site.

To maximize comparability, methodology for plant community quantification followed as closely as possible the methods used by previous studies of uacaris (Ayres, 1986a; Boubli, 1997a), though some modifications were needed because of the exigencies of the igapó habitat (Ayres worked in várzea, Boubli almost entirely in forest

types that flooded neither extensively nor regularly). Quantitative plant methodologies were tested in two initial plots (Quadrats 1 and 2) in 2005.

In all habitats, the four corner points of each quadrat were recorded using a Garmin 60 SCx (Garmin AT, Salem, OR, USA), a GPS unit that is sensitive under dense canopy (Boyle, 2008). Trees whose trunks straddled a plot boundary were only included if the trunk mid-point lay on the plot side of the boundary line. The positions of each quadrat are shown on Fig. II-5. Quadrat methodology is presented in Table II-3.

Table II-3: Quadrat Methodology

Activity	***Description***
Prepare study site	Divide study site into ten numbered blocks, delineating each block with brightly-coloured cord tied to trees or a stake each corner point. Blocks were 25x10m for all quadrats except the igapó margin samples, where 25x5m blocks were used.
Identify trees	All trees ≥ 20cm DBH (diameter-breast-height) were identified to species (with canopy reaching palms, lianas and vines were also included even if DBH < 20cm)
Tag and measure trees	As measuring and identification proceeded, sequentially numbered aluminium tags were attached to each included plant, and its DBH and nearest-neighbour-distance (NND) recorded.
Canopy heights	Canopy height and diameter was also recorded at later dates using laser rangefinder (Yardage Pro 450, Bushnell, Overland Park, KS, USA: accurate to 1m, minimum distance 4m). Trees were selected to give the widest possible range of canopy-DBH data for each species. A minimum of 5 trees per species was used (for rare species, if fewer than 5 individuals were in the quadrats, data were obtained from trees encountered outside the quadrats, but within the study sites).

This methodology excluded hemi-epiphytic trees such as *Clusia* (Clusiaceae). This methodological oversight (shared by previous studies of uacari diets) meant that selection ratios for plants with this *bauplan* could not be calculated. As *Clusia* parts are eaten by uacaris (Chapter 5), inclusion of such plants is recommended for future studies, as is the inclusion of the fully epiphytic vascular flora (especially Araceae and Bromeliaceae).

2.6.2 Phenology - quadrats

Once the quadrats were established, they were visited once-a-month and the phenophase of each tree established. Each canopy was observed with Minox 10x42 binoculars (MINOX GmbH, Wetzlar, Germany). Categories used to record phenological status (phenophases) are given in Table II-4.

Table II-4: Phenological Categories by Plant Part

Plant part	*Phenophase recorded as*
Leaves	New, Mature, All absent
Flowers	Present, Absent
Fruit	Present, Absent

The proportion of the canopy covered with flowers or fruit was assigned to 'light', 'medium' and 'heavy' categories depending on what of the proportion of the full potential space which, in that species, fruits or flowers *could* occupy was currently being so occupied. For leaves, the proportion of the canopy covered by various leaf phenophases was visually estimated in 5% units (i.e. 0, 5%, 10%, 15%). All percentile and categorical assignments were double-checked *in situ* with a field assistant.

Presence of defoliating caterpillars was also noted, to avoid confusion of such induced leaf-lack with natural leaf abcission. In primate diet studies 'buds' are a commonly included phenophase category (e.g. Chapman & Chapman, 1996). However, after some initial attempts, it was realized that buds could not be recorded consistently across all terra firme and igapó tree species and so registration of this phenophase category was abandoned. If, during a phenophase visit, a canopy could not be seen (because of the presence of another tree, or of a vine), a 'not possible' was recorded. I noted all marked trees in the study plots that either died or were killed by tree falls during the study period.

Phenophases have been shown to be strongly connected to timing of inundation in igapó plants (e.g. Maia, 1997; Maia & Piedade, 2000, 2002a,b,c; Maia *et al*., 1998), and

of rainfall in terra firme (Haugaasen & Peres, 2005a; Peres, 1994a) Consequently, river height and rainfall data collected at the Fundação Vítoria Amazônica's (FVA) Seringalzinho research base (grid ref. 01º50.452''S, 61º 35.595''W), were accessed from the data base held by FVA in their Manaus offices.

2.6.3 Phenology - phenotrails

The quadrats did not contain all plant species present in the study area. In addition, while it is common for rainforest species to have highly synchronous phenologies (Adler & Kielpinski, 2000; Poulin *et al*., 1999), there is often some intraspecific asynchrony (Franklin & Bach, 2006). Therefore the methods of Wich & van Schaik (2000) were followed, and quadrat-based phenologies were supplemented with transect-based studies, where fruits and flowers that have fallen to the ground are noted and the species identified. Each month a minimum of three such trails were conducted in both terra firme and in igapó. For each I walked or paddled regular 1km transect and along it I recorded the number and identity of species seen fruiting, flowering or with new leaves. The trail was approximately 2.5m wide (length of my arm + seed spoon [see below] on either side of the canoe). I also identified any fruits and flowers on the ground or water surface. For each individual species I made both quantitative and qualitative estimates of the phenophase intensity. For individual trees I recorded the various phenophases as ``sparse, common, abundant'', while for material fallen and either lying or floating, the absolute number of the flowers or fruits was tallied for each species, and allocated to one of the following categories: sparse (1-10 fruits or flowers), uncommon (11-40), common (41-75), abundant (76-99), super-abundant (100+). New plants (or their flowers or fruits) recorded in this way were collected and identified using the fieldguides listed in Section 2.8. To avoid *cauixi* (a contact dermatitis and-or conjunctivitis caused by free-floating

spicules of freshwater sponges: Machado, 1947), special 'seed-spoons' were constructed with which to fish floating seeds from the water safely (Fig. II-6).

Fig. II-6: Floating Seeds in Igapó, and a Seed Spoon to Access Them Without Eye-Infections

2.7 Crop Volumes

2.7.1 Fruit

A variety of methods has been proposed for measuring the amount of fruit on a tree (e.g. Milton *et al.*, 1982; Peters *et al.*, 1988), focusing variously on the number, distribution in the canopy, or weight of the fruits, and there has been debate of the relative merits and superiority of the various techniques (Chapman *et al.*, 1992 provide a discussion). However, because of the great variety of fruit sizes, shapes and clusterings, as well as the great variation in how visible and accessible fruits might be, Chapman *et al*. (1992) suggest that the simultaneous application of a variety of methods was the most appropriate course. This rationale was followed in the current study and five different methods of measuring crop volume were deployed. These are given in Table II-5.

The chosen method was applied to a minimum of four randomly selected individual trees of each species within the study area. For all techniques (except the last), sampling continued until either 500g of fruit had been obtained or 100 fruits collected. These data were then used as a basis for species and community-based crop volume calculations

(Table II-6). Estimates for each species were made at the time of the year when the plants were bearing fruit at the developmental stage that the uacari was known to eat.

Table II-5: Different Methods of Assessing Crop Volume (after Chapman* et al., *1992)

Action	*Used for*
I: Direct total counting, count all fruits in a canopy	Species with large fruits and small low crowns, e.g. *Eschweilera tenuifolia* (Lecythidaceae).
II: Direct sub-sample counting, count the fruits present on a number of branches (normally 7), average the number of fruits on the sample branches and then multiply-up by the total number of branches in the canopy	Species with smaller fruits and low crowns, e.g. *Macrolobium acaciifoium*, Fab: Caes.; and for species with large fruits and tall crowns, e.g. *Swartzia acuminata* (Fab: Caes.).
III: Collecting from branches, collect one or several branches, count the number of fruits there, then multiply-up by the number of branches in the canopy of the study tree	Medium-sized fruits from tall trees with large canopies, with many small fruit closely grouped together, e.g. various members of the Combretaceae, Lauraceae, Olaceaceae and Sapotaceae
IV: Collecting from entire tree, shake the tree canopy until the fruit stopped falling out, collect all fallen fruit and weigh them. Count the number if a weighed sub-sample and multiply-up	Tall trees with small fruits that could not be climbed safely, e.g. various members of the Combretaceae, Lauraceae and Sapotaceae.
V: Cluster count, take a sample of 10 clusters of fruit and average the number. Then direct count the number of clusters and multiply-up for per-tree total.	Used for taquari (*Amanoa oblongifolia*) and seringaí (*Mabea nitida* - both Euphorbiaceae), and *Diospyros* (Ebenaceae) which have clusters of cherrytomato-sized fruit, and species with clusters of small (<0.5cm) berries (e.g. Myrtaceae and Melastomataceae).

Table II-6: Crop Volume Calculations

Aim	*Method*
Calculate mean crop volume per m² of canopy, for each chosen tree species.	Calculate canopy diameter (method depended tree height: comparison with 3m canoe for low canopies, measure with laser rangefinder for tall ones). For simplicity, assume each canopy is a regular hemisphere, with equal branch structure throughout. As the canopy is a half-sphere, surface area was calculated with $4\ \pi r^2 /2$ (since fruit was borne only on the canopy's outer surface).
Calculate crop weight per hectare	Multiply crop weight per m² of canopy, by number of trees per hectare (from quadrat data), using recorded relationships between DBH and canopy diameter for each species as a correction factor when calculating the total canopy of each species. Correct for breeding system (assume dioecious species will average 50% less standing crop, and for phenology – using phenophase proportions from phenological data for 100% of individuals for non-dioecious species and for 50% of the trees for dioecious ones)
Calculate crop weight for each species in the study site	Calculate proportion of igapó in 5km² study area around research base (using satellite photos from FVA) and, using values above, calculate likely standing crop for each studied tree species. Igapó tree species differ in inundation tolerance (Chapter 1) and so tree community composition is not uniform across the habitat but is banded. Estimating the area any species is likely to occupy within a given igapó block, provides a further correction factor. Calculations (using these factors) will give Individual Crop Volume (ICV) for each species
Calculate crop weight for the study site	Summing ICVs for all target species combined, gives Total Crop Volume (TCV) for the study site at one moment in time. An estimate of the fruit resources available to the uacaris (and their competitors).

All species studied had single-layered crowns, circumventing the complicating factors of within-canopy variation in fruit quality and quantity observed by Houle *et al.* (2007).

2.7.2 Flowers

Uacaris are known to eat flowers (e.g. Ayres, 1986a). Different methods were used to estimate the number of flowers available for the two most commonly eaten species. Flowers of the macacaricuia tree, *Eschweilera tenuifolia*, were enumerated by counting the number of inflorescences in a canopy of 10 randomly selected trees, and then, since uacaris only eat open flowers and there are only ever 1-3 open flowers per inflorescence, multiplying by 2. Measures from the same trees were made during both the 2007-2008 and 2008-2009 flowering seasons. The second species, *Codonanthe crassifolia* (Gesneriaceae), is a small creeping vine that grows adpressed directly on the bark of igapó trees (Fig. II-7). Direct counts of flower number were made for 23 individual plants and the area covered by each was estimated. The nature of its growth-form meant that *Cononanthe* had not been included in the quadrat quantification, so the number and size of *Codonanthe* plants growing on 100 trees was measured across three sequential days' paddling in the four separate areas of igapó. Because of the difficulty of separating individuals in large clumps, an estimated sum total of *Codonanthe* coverage was taken. This included all individual plants, contiguous or not. Plants below 5cm length were never observed to flower, so separate individuals below this size were excluded. Patch sizes were estimated in 25cm² increments from 5cm upwards. For *Codonanthe* on each tree, flowers were recorded on a presence/absence basis. Uacaris also ate the flowers of *Passiflora* cf. *phellos* (Passifloraceae). However, this is a high canopy vine, and reliable estimation of floral crop volume were prevented by visibility problems.

Eschweilera tenuifolia (Lecythidaceae)

Codonanthe crassifolia (Gesneriaceae)

***Fig. II-7: Examples of Flowers Eaten by* C. m. ouakary**

2.8 Collecting and Identifying Plants

2.8.1 Identifying Plants

All plants collected in quadrats, those encountered as fruits or flowers on phenotrails, and those noted as a result of observing feeding activities, were identified as far as possible (normally to family and genus) in the field. This was supplemented with *ad libitum* collections of tree, vine and shrub species encountered in flower or fruit in terra firme and igapó. In the field, Gentry (1993), Ribeiro *et al.* (1999), and van Roosemalen (1985a) were used to identify plants to species. In addition, Mori & Prance (1990) was used for zygomorphic Lecythidaceae, Pennington (1990) for Sapotaceae and Pennington (1997) for the genus *Inga* (Fab.: Mim.). Local vernacular names provided by guides were cross-checked with Freitas da Silva *et al.* (1977, 2004). Guidance on botanical terminology was provided by Harris & Harris (2001) and Jackson (2004). Following preliminary identifications using these resources, exsiccates were made for later herbarium use, and all specimens photographed with a digital camera. These preliminary identifications were later checked by Welma Souza (INPA, Botany and U. Federal Amazonas, Botany) comparing field-prepared exsiccates with the collections of the INPA Herbarium, Manaus. In some cases, identifications were achieved or confirmed by sending digital

images to acknowledged experts in the particular taxa. The plant families, and experts involved, are given in Appendix I-1. In addition, Welma Souza visited all the quadrats to check initial identifications of all sampled trees therein.

2.8.2 Identifying Consumers

This was done by direct observation and by collection of fruits found floating or fallen beneath trees where uacaris had been seen feeding, or in areas in which they had been active within the last 48 hrs.. Found items were identified as having been eaten by uacaris after comparison with a reference collection of material known to have been eaten by parrots and macaws (Fig. II-8), squirrels, terrestrial rodents, *Alouatta, Cebus,* and *Saimiri.* Pitheciine bite marks are very characteristic and the potential exists for confusion between those of *Cacajao* and the other two large pitheciines, *Chiropotes* and *Pithecia*. *Chiropotes* is absent from Jaú (Barnett *et al*., 2002). *Pithecia pithecia chrysocephala* is present at Jaú. However, its canines are both smaller and thinner than *Cacajao* (Hershkovitz, 1985, 1987a,b), and marks I have seen previously on fruits eaten by *P. p. pithecia,* an animal the same size and morphological configuration as *P. p. chrysocephala*, make me confident that I would have been able to distinguish between foods eaten at Jaú by *Pithecia* and *Cacajao*. As it was, during the study I retrieved no feeding material that with what appeared to me to be have been eaten by sakis, and sakis were only ever seen twice in the entire 19 month field period.

Securidaca sp. (Polygalaceae)

Fig. II-8: Species-specific Fruit-damage Patterns: Fruits Eaten by Uacari (upper left) and Macaw (lower left). Entire fruit (right)

2.8.3 Diet Item Classification

All diet items were identified to type (e.g. whole fruit, fruit pulp, aril, seed, leaf, leaf base, pith, bark, flower bud, flower, flower stem, fungus, dead wood, non-plant material), and state of maturity recorded as 'ripe' or 'unripe' where appropriate. Non-plant material was sub-divided into larva in rolled leaf, stem borer, insect in seed, insect in fruit pulp, free-ranging arthropod. In addition, the proportional contributions of leaves, seeds, flower, animal food and other were calculated.

2.9 Quantification of Diet Item Characteristics

The absolute abundance and spatial distribution of foods has been shown to be influential in ordering diet item choice preference of many primate species (Heiduck, 1997; Marsh, 1981; Milton, 1979). However, a number of other criteria may also be influential in diet

item selection (Zhou *et al*., 2006), including such physical attributes as size and hardness (Kinzey & Norconk, 1990; Lambert *et al.,* 2004), and nutritional value (Felton *et al.,* 2009; Milton 1979; Rothman *et al*., 2007), energetic content (Wasserman & Chapman, 2003), presence of defensive compounds (Chapman & Chapman, 2002; Glander, 1982), and time and energy costs of required processing behaviours (Dew, 2005). Chemical aspects of the diet were not investigated by the current study, which focused instead on investigating fruits for an array of physical properties. Fruits included those eaten by uacaris, plus those of species that had never been observed forming part of the uacari diet. The properties investigated were: physical properties (length, width, weight, skin colour, penetrability of pericarp and of sutures (if present), dimensions and weight of seed); presence of physical defences (such as spines, latex).

2.9.1 Measurements

The length and width of fruits, and thickness of the fruit wall were measured to the nearest 0.1mm using SPI 2000 dial calipers (Swiss Precision Instruments, Garden Grove, CA, USA). In keeping with the idea of trying to gain data that would reflect as accurately as possible the experience of the uacari, botanical subdivisions of the part of the fruit external to the seed were ignored, and the fruit wall or pericarp (that is, the entire combination of exocarp-mesocarp-endocarp) was measured as a single entity.

2.9.2 Bite Type and Location

Preliminary observations in 1999, 2000 and 2005, revealed golden-backed uacaris rarely ingested whole fruits. Even small fruits (i.e. those of less than 0.5cm diameter) are generally opened fully and the seed or seeds dentally extracted. Seed extraction is almost ubiquitous in larger fruits. Once seeds are extracted, the fruit is dropped, and could be

retrieved and length, diameter and thickness measured. Size of eaten seed(s) could generally be obtained by measuring the residual lumen or, in multi-seeded fruits, the size of those that remained. Table II-7 gives protocols used when collecting eaten fruits.

Table II-7: Fruit Collecting Protocols

Activity	*Study*
Collecting eaten fruit	Any uneaten fruits that were found amongst these whose seeds had been eaten were collected, and the thickness of pericarp and penetrability was measured separately to allow comparison between eaten and uneaten fruits.
Location at which the tip of the uacari tooth generally leaves a peristent impression on an opened fruit	To test the null hypothesis that marks will be equally distributed across the surfaces of a series of conspecific fruits, irrespective of whether the fruit is dehiscent (has sutures) or indehiscent (no sutures), the location of such marks was recorded for each diet species.
Bite form	In some species all the fruits of a species would not be eaten in the same way; when this happened some were bitten along longest axis, and some bitten across it. Under such circumstances, the relative numbers in each class were recorded, and attempts made to note features of the morphology (e.g. orientation of latex canals and presence of non-uniform thickening) of the fruit that might explain the observed proportions.

2.9.3 Colour

Pericarp colour was recorded for fruits using Munsell Color Charts for Plant Tissues (Munsell Color, New Windsor, NY, USA). This, measuring three variables (*hue* – the colour family, e.g. red, blue; *chroma* – the level of saturation and *value* – the brightness, compared to a neutral grey comparitor shade), provided an unambiguous measure of the exact shade of the pericarp (Fig. II-9).

When coding for insertion into the Excel database, these colours were grouped and simplified into:

- *1, pale (white, yellow, orange)*
- *2, green*
- *3, red*
- *4, dark (blue, purple, black, brown)*

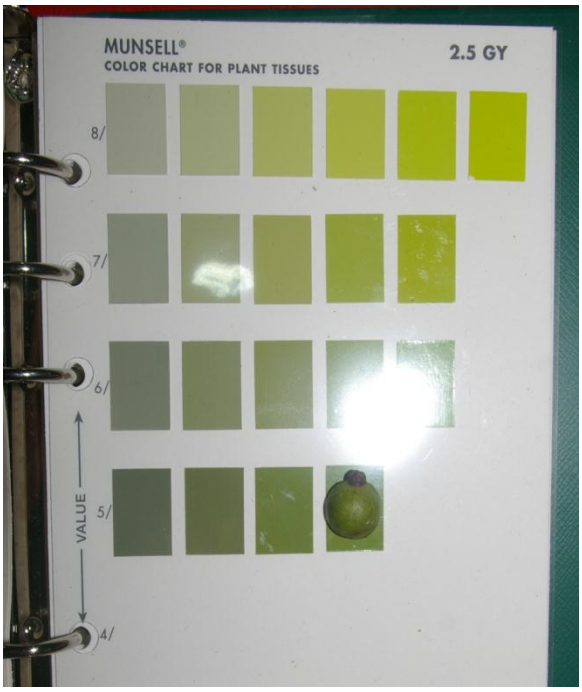


Fig. II-9: Using Munsell Color Charts to Assess Fruit Colour

When the colour of the mature fruit was different from that of the immature fruit, the colour was recorded for the stage that the uacari ate. When the fruit had an indumentum (covering of hairs) of a different colour to that of the pericarp surface (so giving the fruit a different apparent colour, e.g. *Diospyros duckeana*, Ebenaceae; *Duroia velutina*, Rubiaceae), then it was the colour of the indumentum that was registered.

2.9.4 Hardness – quantification

In fruits the force needed to penetrate the pericarp can be measured accurately (Yang & Mohsenin, 1974) using a fruit penetrometer (International Ripening Company [IRC], VA, USA), a device where the force needed to push a spring-mounted rod through the test material is registered and measured on an analogue dial (Fig. II-10).

Most primates use their molars to break open resistant foods (Swindler, 2002), but, uniquely among primates, pitheciines (including *Cacajao*) use their canines (Kinzey,

1992). Thus, while the flat slightly convex end of the commercially-available penetrometer rod end might be mechanically equivalent to a molar cusp, it does not imitate the pointed end of a uacari canine (Fig. II-10). Consequently, there was concern that deployment of the well-established and standardized procedures of measuring fruit resistivity with a penetrometer (e.g. Artes & Escriche, 1994; Breene *et al*., 1974) might lead to over-estimation of the force required to fracture the fruit pericarp. Accordingly, a dental cast of a *Cacajao* canine was taken from a female in the collection of the University of California, Berkeley, Museum of Zoology. The cast was then converted (at San Ramon Dental, CA, U.S.A) into a screw-reamed metal canine prosthesis that could be mounted on the IRC penetrometer and used in place of the rod provides in the standard IRC kit. The now-customized penetrometer was then mounted on a test rig for finer control and greater accuracy of measurement (Fig. II-10). Modelled on the original Fridley Fruit Firmness Tester (Fridley, 1966), the rig was purpose-made for the project by Marapanin Industria e Serviços Técnicos ltda., Manaus, Brazil. Using this set-up, the penetrability of a minimum of 10 examples of each fruit was then measured. To do this, punctures were also made at pre-selected points across the pericarps of selected species of diet and non-diet species, kept constant across species to maximize comparability. Methods used to test whether sutures required a lower force to penetrate than other parts of the fruit surface are given in the next section. Force was measured from the gauge in increments of .01kg. The impacting area of the canine tip was calculated at 1mm^2.

Standard Pentrometer head, and *Cacajao* prosthetic canine

Prosthetic canine mounted on standard fruit penetrometer

Fig. II-10: Equipment for Quantifying Fruit Penetrability

Test Rig, following the original Fridley Fruit Firmness Tester design of 1966

Fig. II-10: Equipment for Quantifying Fruit Penetrability (contd.) - 1

2.9.5 Differential Penetrability of Sutures

Dehiscent fruits have a zone where all or part of the pericarp breaks open to permit release of the seed(s). This zone is known as the 'suture' or 'sulcus' (Harris & Harris, 2001), and represtents a zone of natural weakness (Müntz *et al.,* 1978). To test the null hypothesis that the suture has penetrability equal to that of rest of the pericarp, five

common species were chosen from those with sulcate fruit that were eaten by uacaris: *Hevea spruceana* (Euphorbiaceae), *Macrolobium acaciifolium* (Fab.: Caes.), *Panopsis rubescens* (Proteaceae), *Parkia discolor* (Fab.: Mim.), *Swartzia acuminata* (Fab.: Caes.).

Penetrability of the suture was recorded with prosthetic uacari canine mounted on a standard fruit pentrometer (described in Section 2.9.4, shown in Fig. II-10), and values compared with those obtained from five other random points on the non-suture part of the pericarp surface. The gape and precise angle at which a canine meets a food item is important in maximizing the speed and energetic efficiency with which the item may be processed (Dumont & Herrel, 2003). In the present study, though the action of a penetrometer-mounted canine will, clearly, not imitate precisely the exact angle in which the food item is bitten under natural circumstances (e.g. Taylor & Vinyard, 2008), nor the exact form in which pressure is exerted in the bite force (Plavcan & Ruff, 2008), the values obtained were assumed to be an acceptable proxy for the differences in bite force that the uacari itself must exert when puncturing the pericarp at sutures and elsewhere on the pericarp.

In each case the force needed to make a mark (equal to penetrating the epicarp), and making a hole (equal to penetrating the endocarp) was recorded for six places on the surface of each fruit. The fruits of all species are large, with at least one dimension greater than 5cm, and hence sites of the various penetrations can be spaced across the surface so that the multiple tests can be assumed not to weaken the husk and result in sequentially diminishing readings. The multiple data points from the surface of the same fruit serve as replicates. This was not, however, true for the suture, where it is was generally only possible to make one measure each of epi- and endocarp penetrability

before the area of natural weakness broke open. Hence, 14 measures were taken from each fruit. This was done for 12 fruits from each of the five species, a total of 820 measurements. For comparative purposes, the method was repeated on a further 12 fruits *per* species, using the standard rounded rod end of a commercial penetrometer.

2.9.6 Differential Distribution of Bite Marks in Uacari-bitten Fruits

To test the null-hypothesis that uacaris bite fruits at random, and do not chose the area of least resistance, I analysed the distribution of bite scars on the surface of fruits from five species of igapó tree. I first tested if, on fruits with sutures, bite marks occurred more frequently along sutures than elsewhere, and compared the location of bite marks on the fruits of five species whose pericarps lacked sutures. Bite scars were scored as '+' if they were within a distance either one side of the suture or the other that was ≤10% of the fruit diameter, or if the bite mark lay directly on the suture itself. Bite marks were scored as '–' if they appeared elsewhere on the pericarp.

2.9.7 Differential Penetrability of Insect-infested and Non-infested Fruits

Hard-husked fruits make up a high proportion of the reported diets for most uacaris (Barnett *et al*., 2005; Bowler, 2007). The mechanical force required to open many of these may be considerable (Kinzey & Norconk, 1990). Insect infestation might weaken fruits, making them easier to open. To test this, the forces required to penetrate infested and non-infested fruits of seringaí (*Mabea nitida*) and taquari (*Amanoa oblongifolia*: both Euphorbiaceae), *Duroia velutina* (Rubiaceae), and *Diospyros duckeana* (Ebenaceae) were compared using the methods given in Section 2.9.4. Infested fruits were recognized by the presence of bore-holes on the surface (Fig. II-11). A minimum of 10 fruits was sampled from each species.

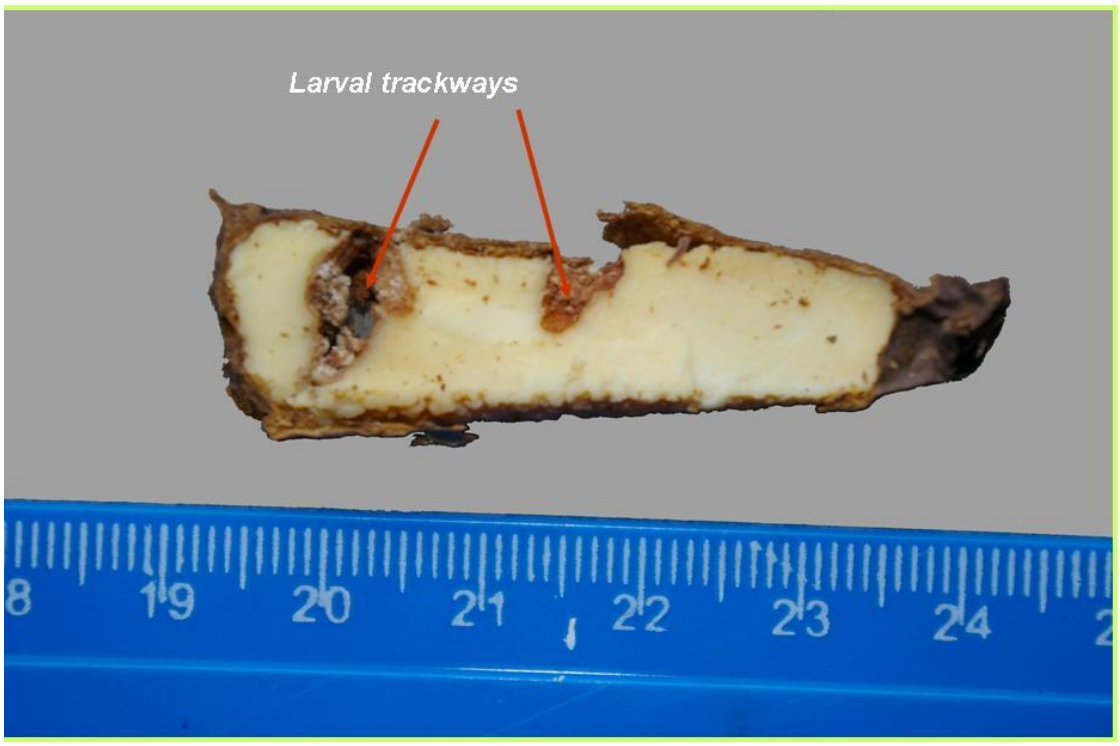
Mabea nitida (Euphorbiaceae)

Fig. II-11: Insect Bore Holes, Indicating an Infested Fruit

2.10 Insects, Insectivory and Fruit Selection

Insects may enter the diet of uacaris either from direct ingestion or their ingestion within the pulp or seeds of fruits, or in other items such as leaves. Insects may therefore influence diet choice by uacaris in three ways: i) by acting as a nutrient supplement that attracts uacaris to the potential diet items that contain them, ii) by attracting the uacaris which then also eat additional fruits (possible for a folivorous insect) and iii) by acting in a defensive role and so repelling the uacaris. There exists a fourth possibility – that insects may be present and have no detectable influence of the frequency of fruit choice or on the ranking of the fruit as a diet item. For i), the challenge clearly is to distinguish between deliberate or accidental insectivory.

Because little was known about *C. m. ouakary* diet when this study began, I did not plan systematic recording of insectivory. However, active insectivory could be recorded during field observations, and chances of registering insectivory were increased with searches for arthropod remains in wild-collected fæces (below). To test insect larvæ were present in fruit available to uacaris, fruits encountered on pheno-trails, or during collection of uacari diet items, were destructively sampled for larvæ during measurement and identification. If a species was found to be infested, then further samples of fruit were gathered and the ratio of insect infested/non-infested fruits was directly enumerated from these. Most fruit-inhabiting larvæ leave marks of their presence, often as tunnels, cocoons, piles of frass or emergence holes on the epicarp surface (Fig. II-11). These features often run though the whole fruit or seed and are not confined to one part. This meant that it was possible to look at fruits uacaris had eaten and see if they had been infested (Fig. II-12). A comparison of the proportions of infested/non-infested on the tree with proportions in the fruit remnants beneath it provided a rough indication as to whether uacaris were actively selecting fruits which contained insect larvæ.



Eschweilera tenuifolia (Lecythidaceae)

Fig. II-12: Larval Insect Tracks in a Uacari Diet Fruit

2.10.1 Identifying Insects in Fruits and Leaves

To identity the insects living in fruits and leaves eaten by uacaris, fruits with marks of infestation were placed on a bed of vermiculite in netted pots. Beatriz Ronchi-Telles (Entomology, INPA, Manaus) then raised the animals to imago status and circulated specimens for identification. Caterpillars collected from leaves and considered to be potential uacari foods were similarly treated. Any imagos emerging in the field were killed and pinned (following McGavin, 1998) and digital images then sent to a series of international experts (Appendix I-2). The weight of infesting insects was calculated as a percentage of the fruit total weight, using a Salter electronic mini-balance (model 1250, Salter-Brecknell, West Bromwich, UK) which weighed to the nearest 0.1g.

2.11 Additional Diet Measures

2.11.1 Fœcal Collections

Uacari fæcal pellets were collected whenever encountered. In practice this was only between May and August. Collection was possible in these months because synchronized leaf fall by igapó trees (Parolin *et al*., 2002) caused widespread seasonal anoxia in igapó waters, and this greatly reduced the feeding and activity rates in igapó-living fish (Chapman, 1997; Scarano & Crawford, 1993). Because of low productivity, much of the material on which igapó fish feed is autochthonous (Sheanan *et al.,* 2005). Consequently, in all other months, once they hit they water, uacari fæces were quickly eaten by fish. No previous published description exists of the appearance of uacari fæces, but we were able to recognize them after a passing female uacari defecated directly into a project canoe – possibly an aggressive display. Subsequently, the pink-grey cuboids were retrieved with either a seed-spoon or plastic bag, transferred to a labeled plastic vial and, at the field station, stored in 50% alcohol.

Collected fæcal pellets were analysed individually in the lab of Beatriz Ronchi-Telles lab, following Putnam (1984)'s methods. Pellets were broken up on a glass petrie dish and, under the 10 to 40x zoom lens of a Leica/WILD 3C binocular dissecting microscope, the entire contents picked through with tweezers and seekers. Solid material was initially separated into 'animal' and 'other', before being more finely categorized. Next separated arthropod parts were categorized first to order and then, where possible to family or below. Percentages of the categories (e.g. ants, cockroaches, termites) were calculated using 0.5cm² graph paper, placed under a petrie dish and with the sorted parts moved to form a contiguous single item layer.

2.12 Observation of Uacaris

2.12.1 General Protocols

On those days devoted to primate surveys, uacaris were searched for either on one of two five-km trails cut in terra firme, or in one of three locations in igapó (Fig. II-5) using a wooden canoe (Fig. II-13).

Fig. II-13: Field Guide Roberto with a Canoe used for Surveys and Sample Collecting

Uacaris were searched for in flooded forest by wooden canoe and on-foot in terra firme. As previous field visits in 1999, 2000, and 2005, and all local knowledge, indicated that uacaris are only present in terra firme when igapó is not flooded, the focus was on igapó between Feb and Sep 2007, and during this period terra firme was only entered for phenological sampling. Additionally, between Dec 2007 and Apr 2008 searches in terra firme were conducted on a monthly basis by a field assistant (the Brazilian biologist Thais Almeida), while I concentrated solely on igapó. Thais Almeida

continued to collect data past the termination of my studies in April 2008, working until Sep 2008. She did not see uacaris in terre firme when the igapó was flooded. In this chapter, these supplementary data collected by Thais Almeida are used only in the section on habitat use, though they do form a part of chapters 5 and 6.

Daily searching began as close to 06.00 as weather permitted. If, on the previous day, the animals had been left at confirmed sleeping trees, I tried to be on-site by 05.30 in order to catch animals rising. Observations were made with 10x42 binoculars and recorded in Rite-in-the-Rain waterproof notebooks (J.L. Darling Corporation, Tacoma, WA, U.S.A) and/or fieldsheets printed on Rite-in-the-Rain waterproof paper. I personally collected field data for 211 days from 15 months across a total of 19 months. Of the 211 days, 170 were spent searching for uacaris, and 41 dedicated entirely to botanical data collection or diet-related work (Chapter 5 and 6). The field work period was divisible into two blocks, the Pilot Period and Main Study. During the former, I followed uacaris and tested field methods with the main focus of habituating the study animals. During the Main Study animals were considered to be habituated and I collected quantitative data. The Pilot Period included 95 field days between Oct 2006 and Mar 2007. The main study included 115 of field days between Apr 2007 and Apr 2008. During the Main Study, I spent 1,096 hrs. in the forest at Jaú, of this I spent 784 hrs. searching for and observing primates, of which 101 hrs 48 mins (6,108 mins: 12.9%) was contact time with *Cacajao m. ouakary*.

Unless vegetation was exceptionally dense and clear observation impossible (in which case we paddled slowly closer), my guide and I stopped as soon as the animals were sighted and began observing them from available cover. If the animals were not nervous

and cover was available, we would try progressively to move closer. Upon initial contact the number of animals in the band, composition (Adult-Juvenile-Young), habitat, current activity (Feeding, Moving, Resting, Other: Table II-8), and group spread were estimated, along with an estimation of proximity to other groups, and if other primate species and/or birds were associated with the band. Height above the substrate was noted and the distance between the monkeys and myself. In all cases visual estimation of distance was aided by measurements with a laser rangefinder (Yardage Pro 450, Bushnell, Overland Park, KS, U.S.A: accurate to 1m, minimum distance 4m).

2.12.2 Behavioural Sampling

Once initial data were noted, quantified data collection commenced. Here, following Ferrari (1988), Instantaneous Scan Sampling (ISS) and focal animal data recording were interspersed with *ad libitum* data collection. This mixed sampling strategy, containing elements of both focal and group sampling, maximizes representativeness of collected data (Fragaszy *et al.*, 1992), as it captures important events that could be missed if only time-based sampling is used. The *ad libitum* portion, for example, allows assessment of events such as time spent processing individual fruits and the rate at which individual fruits are ingested – something that would be very difficult if scan methodology had been used exclusively.

Once animals were contacted, an ISS (Altmann, 1974) was made to categorize the activity state of the band. Field-testing in 2005 and during the habituation period of 2006-2007 showed that, because of the speed at which animals moved in the canopy as well as inter-individual distances that often exceeded 10 body-lengths, it was hard to record data reliably from more than three uacaris simultaneously. Consequently, if band size

exceeded three, the nearest three animals were chosen from the band and ISS conducted every 30 seconds for five sequential minutes following contact, with each of the three chosen animals being sequentially point sampled at 30 second intervals for the entire five minute period. This gave a maximum of 33 records (i.e. 11 *per* animal) during each 5 minute period of multiple focal animal sampling. If, during this time, any target animal was not visible at the moment of recording, that record was marked as 'out of sight'. If no animals were visible for three sequential scans (i.e. 3 x 30-seconds) then the observational block was terminated. One minute intervals separated observational blocks, during which *ad libitum* behavioural sampling took place. Then, after a 5-second pause to guard against picking the most visible behaviour, observations began again. The 5-minute block began even if only one animal was visible. If one or two additional animals became visible, they were added in for the remainder of the five minute period. It was not possible to identify individuals and timid animals may therefore be under-represented in the sample. Supplementary *ad libitum* observations of uacaris were made when encounters occurred but logistic considerations meant that the structured observations listed above were not possible. Notes were also made on events of interest, such as reaction to other species (small birds, parrots, raptors, other primates). Categories for observed behaviors are given in Table II-8.

Table II-8: Categories for Observed Behaviours

Category	*Sub-category*	*Observation*	*Observation sub-class and definition*
Feeding	Procuring	Food type (leaf, flower, stem, fruit, arthropod, vertebrate, other)	How procuring *visual searching* -: moving back and forth, obvious intense visual contact with immediate substrate; *manual searching* -: *fossicking*: small-scale movement of hands within the food-item containing substrate, or *plucking*: manually or dentally removing the food item from its original site on the plant.
	Processing	Food type (leaf, flower, stem, fruit, arthropod, vertebrate, other)	How processing -: *holding and manipulating*: food item free of parent plant held in hand or hands, either passively or being opened by fingers *dental manipulation*: fruit held up to mouth by hand or hands and contact occurring with either incisors or canines *masticating*: movement of jaw and of temporalis muscles indicative of molar-based trituration occurring.
Moving	Foraging	How foraging	*Pluck*: as above; Fossick: as above; *Grab*: a rapid pouncing movement of the arm culminating in a swift closure of the hand around an item. Not accompanied by a pause in on-ward movement.
	Travel	How moving	*Walk*: Quadrupedal movement, with three hands-feet in contact with the substrate at any one time *Run*: Quadrupedal movement, with two hands-feet in contact with the substrate at any one time *Leap*: No hands or feet in contact with a substrate (combines horizontal leaping and vertical movements [controlled falls])
Resting – individual behaviour	Sleep Rest, Self-groom Vigilant	Position in canopy where event occurred: close to main trunk, middle of canopy or canopy edge.	No. involved in grooming, reciprocity observed?
Social Behaviour – interactions with others		Social behaviour - adult	groom/play/aggression/mate/sleep
		Social behaviour - independently locomoting juvenile	groom/play/ aggression/sleep/interact with mother

Data were manually recorded on a data sheet photocopied onto plasticised Rite-in-the-Rain paper (J.L. Darling Corporation, Tacoma, WA, U.S.A). Behaviours of infants were not recorded quantitatively, but were the subject of qualitative notations.

When recording behaviours during ISS, a 5 second lag time was left between seeing the animal and recording its behaviour, to guard against over-recording highly-visible behaviours. Uacaris are almost entirely arboreal (Results, Chapter 4). So, for 'moving', I recorded the thickness of the used arboreal substrate, as well as its height above the ground (or water surface), and the maximum height of the canopy the animal was seen in.

Notes were also made on the time required to process individual items, and I recorded the time taken to remove a diet item from the tree, time required to process it so that could be put into the animal's mouth, duration of period in the mouth (when an animal was feeding this effectively became time between one item being put in the mouth and the next being reached for, times therefore being calculated only to the penultimate item).

2.12.3 Defining 'feeding record'

Observational information on diet was obtained by combining scan and *ad libitum* sample data. This was supplemented with data from fallen fruits. Each eaten fallen fruit was treated as a single feeding record. When calculating the number of feeding records from observational data, it was important to achieve parity between informations derived from scan and *ad libitum* samples. Because there were 30 seconds between one scan and the next, the duration of any continuous feeding record derived from *ad libitum* observations was divided into 30 second portions: feeding events observed under *ad libitum* conditions that lasted, say, 31 and 59 seconds, both became two feeding records

The combination of three different methods of sampling to provide feeding record totals may, at first, appear a questionable methodological practice. It can however, be defended on the following grounds:

- the approach has been used in previous primate studies on *Cacajao* (Ayres, 1986a; Boubli, 1997a; Bowler, 2007), as well as for dietary studies of *Chiropotes* (Veiga, 2006; Pinto, 2008), the genus of living primates most closely related to *Cacajao* (Canavez *et al*., 1999), and the one with which ecological comparisons are most frequently made (Ayres, 1981, 1989; Norconk, 2007).
- Feeding records from scan and *ad libitum* studies were comparable since processing of individual items (such as a piece of pith, a flower, or the extraction of an individual seed from a multi-seeded fruit) was sufficiently rapid to be recorded as a single record by both methods.
- Scans occurred every 30 seconds. The division of *ad libitum* data into 30 second aliquots provided parity with these observations. It avoided inequalities that would occur if an animal were feeding on an item that took more than 30 seconds to process. Without this adjustment an item could count as two feeding records in scan-based observations, but just one feeding record in *ad libitum*-derived data.

The methods used doubtless underestimated some categories: species with fruits that sank will have been underestimated in debris samples in the flooded igapó, while consumption of adults and larvæ of colonial insects represented an especially acute problem, as the entire nest was counted as one record if found as debris. Insectivory is

widely considered to be an underestimated portion of the diet of uacaris, in both flooded (Bowler, 2007), and unflooded (Boubli, 1997a), habitats, and this methodological problem can only compound that.

2.12.4 Diet Item Categorization

The categories used when classifying diet items are given in Table II-9.

Table II-9: Diet Item Categories

Category
Flowers (petals/nectaries/whole/other)
Fruit (pulp/seed/whole); seeds; insects
Leaves (young/old/lamella/petiole)
Animal matter
Bark/wood
Unknown.

Diet items were identified either from direct observation or from collection of dropped material. If the species was not already known to me, then samples were collected for botanical voucher specimens and the process of plant identification begun. Eaten material was generally photographed *in situ* with a digital camera (originally an Olympus Stylus Digital, later a Samsung GX-1), and its identity recorded on a field-portable whiteboard.

2.12.5 Classification of Fruit Ripeness Categories

Uacaris are known for the high proportion of unripe seeds in their diet (Norconk, 2007). To ensure that ripeness classifications were not biased by expectations, I studied fruits *in situ* during three preliminary visits to the Jaú field site. These visits (made in 1999, 2000 and 2005) permitted me to become acquainted with almost all the families and genera that I anticipated golden-backed uacaris would eat, based on studies of *Chiropotes* diet (Ayres, 1989; Ferrari, 1995; Kinzey, 1997; Kinzey & Norconk, 1990, 1993; Peetz, 2001; van Roosmalen *et al*., 1981, 1988), and of *Cacajao* (Ayres, 1986a, 1989; da Cunha & Barnett, 1990; Heymann, 1990; Aquino & Encarnatíon, 1999; Boubli, 1997a). In fruit,

visible changes in the maturational states generally involve changes in fruit size, and in the colour and the hardness of the pericarp. Because the three preliminary visits covered both the wet and dry seasons, I had become acquainted with the maturational states of the majority of the fruits involved, and hence I was able to categorize ripeness of samples of the diet of *C. m. ouakary* when collecting them. Prior to the current fieldwork, I had not encountered germinating seedlings in the uacari diet, but their appearance was sufficiently characteristic to allow their unambiguous assignment to this category.

2.12.6 Calculating Proportional Contribution to the Diet

Proportional contribution to the diet was estimated in two ways; 1) the number of individual food items seen being eaten during scans and *ad libitum* observations, 2) the number of individual food items encountered in feeding debris. The problems associated with approach (1) are the under-representation of items eaten very quickly and the failure to identify small items so that they end up in the category 'Other'. The problems associated with approach (2) are that items which sink will not be retrieved when sampling is occurring in igapó, plus the absence in the debris of those items that are eaten entire, or which cannot be identified firmly as having been eaten by uacaris. To group eaten objects for analysis, I divided them taxonomically (to species in almost all cases, to genus and morpho-species in some taxonomically-challenging families such as Myrtaceae and Sapotaceae). Eaten objects were allocated to one of 17 diet item categories (including young leaf, flowers, mature leaves, flowers, immature seeds and whole fruits).

Each eaten object was considered a 'diet items', a distinction in which each anatomically distinct part was considered as a separate entity (e.g. young leaves, flowers, immature seeds of the same species constitute three diet items).

2.13 Calculating Selectivity Indeces

2.13.1 General Observations

Selectivity indices have been widely used in diet studies, and seek to quantify the extent of the non-random nature with which animals exploit available food resources (Wrangham *et al.,* 1996; Ramos-Fernández & Ayala-Orozco, 2003). The occurrence against which frequency in the diet is most often compared is the relative abundance of the diet species in quantative botanical inventories (e.g. Ayres, 1986a, 1989; Boubli, 1997a). In the Ivlev Index used in the current study (Ivlev, 1961), a 1:1 ratio between abundance in diet and environmental abundance of the resource indicates that it is exploited at the frequency at which they are encountered in the environment, while above 1 indicates positive selection, and below 1 indicates avoidance (Pinto, 2008).

2.13.2 Factors Influencing Selectivity Indices

In addition to socio-cultural and nutritional factors potentially involved in primate diet, and those involving crop volumes and fruit size and pericarp thickness and penetrability (Section 2.9), a variety of other physical features of fruits may also be influential (Dew, 2005; Kinzey & Norconk, 1993; McConkey *et al*., 2002; Stevenson, 2004). The physical features recorded in the current study are given in Table II-10. This includes material collected by direct observation and that collected from phenotrails.

Table II-10: Physical Aspects of Fruits Recorded in this Study

Aspect	*Record*
Spines or urticating hairs	presence/absence, location on plant
Presence of latex in eaten part	if sticky, caustic, both
Ants	presence in species, percentage of trees with ants

It is well established that primates track resources over both space and time, apparently recalling both locations of fruiting trees and when they will produce fruit of the appropriate maturation stage (e.g. Stevens *et al*., 2005). However, if a tree species that is being eaten for its fruit is dioecious, then the effective number of trees (from the primates' point of view) will be less than the number of trunks of that species counted in a quadrat. Exactly how much less will depend on the ratio of androecious (male) plants to gynoecious (female, fruit-bearing) ones. Time pressures meant it was not possible to investigate plant sex-ratios in the field. Instead, I used the specialist family floras from the *Flora Neotropica* series, complimented, where needed by genus-specific sources. These appear in Appendix II-4.

2.14 Feeding Trees

Trees where uacaris had been seen feeding were tagged with orange fluorescent tape (Forestry Supplies, Jackson, MS, U.S.A) and sequentially numbered. As soon as practical after a feeding observation in a tree, data were collected for that tree (Table II-11).

Table II-11: Data Collected for Each Feeding Tree

Data type
Species identity
DBH (to nearest cm)
Max. canopy altitude (measured to top of visible canopy)
Max. canopy diameter
Tree an emergent? (if so, by how many m?)
Status of surrounding canopy (broken, continuous etc.)
Distance to river (if tree in igapó or borokotò)
Distance to igapó (if tree in terra firme or capoeira)
Distance to nearest feeding tree (from the same day's feeding records)
Species identity and phenophase of 25 trees nearest to feeding tree
Radius of the sample for the 25 trees

Distances were quantified with a laser rangefinder, diameters with a metric tape. GPS data were retrieved originally with a Garmin eTrex, and then again with a Garmin

60SXc at those locations where dense canopy cover had prevented the eTrex from making satellite contact.

2.15 Sleeping Trees

When uacaris were observed sleeping in trees, either during the day or at dusk, data were taken to permit the characters involved in the selection of sleeping trees to be determined. The characters measured are given in Table II-12.

Table II-12: Data Collected for Each Sleeping Tree

Data type
Species identity
DBH (to nearest cm)
Max. canopy altitude (measured to top of visible canopy)
Max. canopy diameter
Tree an emergent? (if so, by how much)
Status of surrounding canopy (broken, continuous etc.)
Distance to river (if tree in igapó or borokotò)
Distance to igapó (if tree in terra firme or capoeira)
Distance to nearest feeding tree (from the same day's feeding records)
Number of sleeping uacaris
Their location in the canopy and distances between them
Tree dead or alive
Presence of lianas

In addition, to provide a comparison of for presence-absence of lianas, a random sample of 100 large trees was surveyed for the presence of lianas, and their presenc and extent categorized as follows:

Table II-13: Data Collected for Each Tree During Liana Survey

Criteria of Liana Survey
Lianas present/absent
If present – density extent (very high: covering >50% of branches; high, covering 25-30% branches; low, 10-24% of branches; sparse, <10% of branch area.
Number of lianas – if possible to distinguish
Aerial or terrestrial contact: if any reaching ground or not.

2.16 Statistical Methodology

To determine the significance of results, a number of statistical tests were deployed, following recommendations in Dytham (2006) and Hayek & Buzas (1997). Some tests were used to address a very specific situation and, being used just once, are mentioned in the appropriate chapter section. The following tests were applied widely:

Chi-squared: to analyse variation of observed frequency distributions from expected values

t-test: used to compare the means of two samples, testing whether they could have come from the same population, when data are parametric

Mann-Whitney U test: used when means were compared (due, for example, to unequal sample sizes), when data are non-parametric

ANOVA: used to compare the means of more than two samples when data were parametric

Kruskal-Wallis: used to compare means of more than two samples, when data were non-parametric.

Data were tested with a Kolmogorov-Smirnov test to determine if they were normally distributed (parametric) or not (non-parametric). Bonferroni Corrections (dividing 0.5 by the number of comparisons made) were used, where required, to correct for the likelihood of over-assessment of significance arising from making multiple comparisons within the same data set. Duncan's 1-way ANOVA was used as a post-hoc test to assess presence of significant differences among multiple independent groups.

CHAPTER 3

THE PLANT COMMUNITY AT THE JAÚ STUDY SITE

The tree is known by his fruit.
Matthew xii. 33.

3.1 Introduction

This chapter describes the species composition, phenology and crop volumes of the plant community in flooded and non-flooded habitats used by the golden-backed uacari during the field study. Data are primarily based on quantitative analysis undertaken in quadrats, but supplemented by data from outside these areas. The purpose of the data is to provide an idea of the nature and extent of dietary resources available to the uacari on a monthly basis and show how these changed over the year. The significance of the patterns of plant community composition and seasonal availability of potential diet items are discussed in the context of the diet (Chapter 5), and the foraging behaviour (Chapter 6), of *C. m. ouakary*.

3.1.1 Methods Summary

Methods for quantification of the plant community at the Jaú study site have been detailed in Chapter 2. In summary, the following were undertaken:

- Quantitative botanical studies of four habitats with 0.5ha plots. Species identified, DBH and NND measured.
- Monthly phenological samples in quadrats
- Monthly phenotrail samples
- Calculation of crop volumes accounting for density of fruits, size of canopy and plant breeding system.

3.2 Plant Community Composition

Analysis of 2061 trees, palms and vines in eight quadrats registered 282 species of trees, palms and vines, in 139 genera from 48 families. Of these, 218 (77.3%) were identified to botanical species, 267 (94.7%) to genus, and 268 (94.32%) to family. Two collected trees not identified to species appear to represent genuine new taxa (either species or sub-species). Lianas are notoriously difficult to identify (Putz. 1984; Gentry, 1993). Hence, while only two species of tree remain unidentified (even to family), 14 of the 19 lianas species remain so. The identity and distribution of plant species in the quadrats is given in Appendix III-1.

There were a total of 89 species (1416 individuals) in all the igapó habitats sampled by quadrats 3, 7, 8 and PG1 and 2. Of these 48 species (942 individuals) were found in the interior three quadrats (3, 7, 8) and 67 species at the igapó forest margin (quadrats PG1 & PG2: 474 individuals). There were 26 species that occurred in both the margin and the interior quadrats. In non-flooded habitats, 127 species (214 individuals) were recorded from borokotò, 48 species (190 individuals) in capoeira and 114 species (241 individuals) in terra firme.

The six commonest (by number of individuals) tree species are listed in Tables III-1 and III-2 list for flooded (igapó) and non-flooded forest (borokotò, capoeira and terra firme), respectively. Table III-1 provides data on the three 0.25ha quadrats (3, 7, 8) from igapó of varying inundation durations, and the two margin samples (PG1 and 2) which, when combined, also total 0.25ha. III-3 lists the 10 largest species in terms of mean DBH for both igapó and all non-flooded forest types combined.

Table III-1: The Six Commonest Plant Species in the Igapó Quadrats

Q3 (No. trees = 361)	***Q7 (No. trees = 276)***	***Q8 (No. trees = 305)***	***Margin (PG 1 & PG2 combined) (No. trees = 474)***	***All Igapó (all quadrats combined) (No. trees = 1416)***
Species (No. trees, % of total)	***Species (No. trees, % of total)***	***Species (No. trees, % of total)***	***Species (No. trees, % of total)***	***Species (No. trees, % of total)***
Pouteria elegans (Sapo) 105 (29.08)	*Buchenavia ochrogamma* (Comb) 91 (54.16)	*Eschweilera tenuifolia* (Lecy) 122 (40)	*Micropholis venulosa* (Sapo) 38 ()	*Amanoa oblongifolia* (Euph.) 150 (10.59)
Amanoa oblongifolia (Euph.) 82 (22.7)	*Myrcia grandis* (Myrt) 23 (13.69)	*Eleoluma glabrescens* (Sapo) 44 (14.42)	*Sclerolobium* sp. (Faba) 34 ()	*Pouteria elegans* (Sapo) 146 (10.31)
Mabea nítida (Euph) 61 (16.89)	*Eschweilera alba* (Lecy) 17 (10.11)	*Amanoa oblongifolia* (Euph.) 41 (13.44)	*Eleoluma glabrescens* (Sapo) 32 ()	*Eschweilera tenuifolia* (Lecy) 137 (9.6)
Homalium racemosum (Flac) 18 (4.98)	*Burdachia prism-atocarpa* (Malp) 14 (8.33)	*Hydrochorea marginata* (Faba) 40 (13.11)	*Amanoa oblongifolia* (Euph.) 27 ()	*Buchenavia ochrogamma* (Comb) 94 (6.63)
Licania heteromorpha (Chry) 14 (3.87)	*Myrcia paivae* (Myrt) 12 (7.14)	*Pouteria elegans* (Sapo) 20 (6.55)	*Duroia velutina* (Rubi) 25 ()	*Eleoluma glabresecens* (Sapo) 92 (6.49)
Hydrochorea marginata (Faba) 13 (3.6)	*Licania heteromorpha* (Chry) 12 (7.14)	*Mabea nítida* (Euph) 12 (3.93)	*Ternstroemia candolleana* (Thea) 25 ()	*Mabea nítida* (Euph) 75 (5.29)
% of Total, 81.16	**% of Total, 60.86**	**% of Total, 88.19**	**% of Total, 38.18**	**% of Total, 49.01**

Table III-2: The Six Commonest Tree Species in Non-flooded Forest Quadrats

Borokotò (No. trees = 214)	***Capoeira (No. trees = 190)***	***Terra Firme (No. trees = 241)***	***All Non-Flooded Forest Types (Borokotò, Capoeira, Terra Firme: No. trees = 645)***
Species (No. trees, % of total)	***Species (No. trees, % of total)***	***Species (No. trees, % of total)***	***Species (No. trees, % of total)***
Attalea maripa (Arec) 11 (5.14)	*Protium trifoliatum* (Burs) 13 (6.84)	*Gustavia elliptica* (Lecy) 17 (7.05)	*Gustavia elliptica* (Lecy) 21 (3.25)
Aniba ferrea (Laur) 10 (4.67)	*Miconia argyophylla* (Mela) 12 (6.31)	*Microphilis guianensis* (Lecy) 11 (4.56)	*Protium trifoliatum* (Burs) 14 (2.17)

Table III-2: Non-flooded Forest Six Commonest Trees – continued 1			
Borokotò	*Capoeira*	*Terra Firme*	*All Non-Flooded Forest Types*
Swartzia tomentifera (Faba) 9 (4.2)	*Miconia poeppigii* (Mela) 11 (5.78)	*Swartzia* sp. (Faba) 8 (3.31)	*Aniba ferrea* (Laur) 13 (2.01)
Caraipa grandifolia (Clus) 6 (2.8)	*Tapirira obtusa* (Anac) 11 (5.78)	*Eschweilera wachenheimii* (Lecy) 7 (2.9)	*Swartzia* sp. (Faba) 13 (2.01)
Pouteria sp. (Sapo) 6 (2.8)	*Virola mollissima* (Myri) 11 (5.78)	*Oenocarpus bacaba* (Arec) 7 (2.9)	*Tapirara obtusa* (Anac) 13 (2.01)
Licania heteropjylla (Chry) 5 (2.33)	*Ocotea nigrescens* (Laur) 9 (4.73)	*Clusia* sp. (Clus) 6 (2.48)	*Virola mollissima* (Myri) 13 (2.01)
% of Total, 21.96	**% of Total, 35.26**	**% of Total, 23.23**	**% of Total, 13.48**

Table III-3: Tree Species with Greatest Mean DBHs above 100cm

Igapó* ***(Mean DBH cm, No. measured)***	***Non-flooded forest habitat types**** ***(Mean DBH cm, No. measured)***
Ocotea sp. (210, N=1)	*Lecythis zabucajo* (450, N=1)
Aniba sp. (148, N=1)	†*Aldina heterophylla* (275, N=1)
Homalium racemosum (143.25, N=4)	*Aldina unifolia* (237, N=1)
†*Hydrochorea marginata* (133.25, N=4)	*Qualea* sp. (237, N=1)
†*Amanoa oblongifolia* (129.8, N=19)	†*Aspidosperma schultesii* (220, N=1)
Quiinea nigricans (129, N=1)	*Osteophloeum platyspermum* (220, N=1)
†*Macrolobium acaciifolium* (123, N=1)	*Aldina heterophylla* (235, N=2)
†*Mabea nitida* (114, N=1)	*Caryocar glabrum* (210, N=1)
†*Pouteria elegans* (113.33, N=8)	*Licania oblongifolia* (210, N=1)
†*Eleoluma glabrescens* (107, N=1)	*Taralia oppositifolia* (203, N=1)
Licania heterophylla (100, N=1)	*Sclerolobium melanocarpum* (166, N=1)

*** *Note:*** species marked with an † were recorded in the diet of *C. m. ouakary*

Figure III-1 compares the distribution of DBHs for individuals of all species of trees, palms and lianas in 10cm increments for flooded and non-flooded habitats.

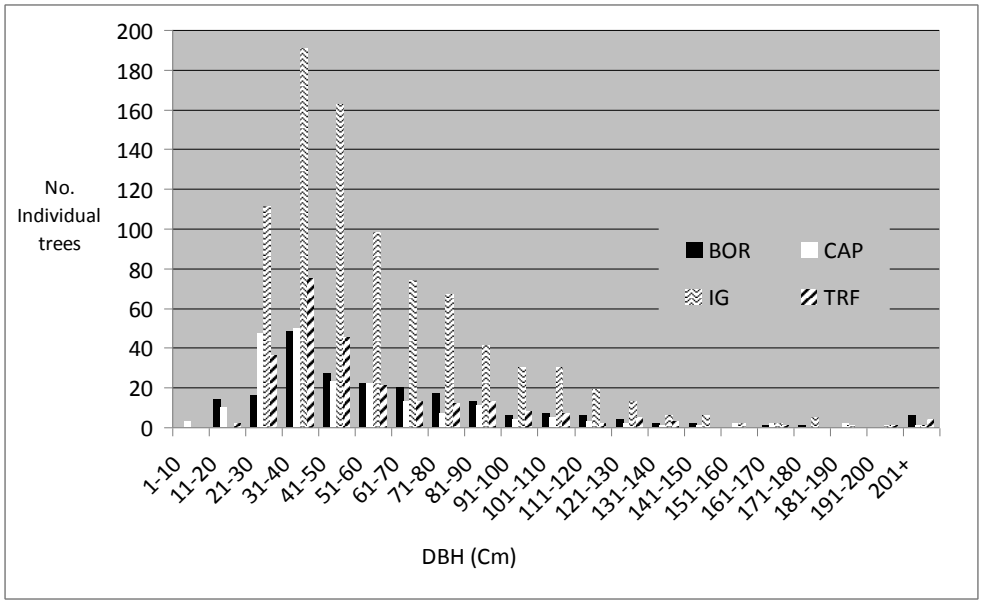


Figure III-1: Distribution of DBH of Trees, Palms and Lianas by Habitat

Table III-4 gives the distribution of trees by DBH in different habitats for four size categories. No trees < 20cm were included, though lianas and palms with DBH less than this were measured.

Table III-4: Distribution of Trees in Four DBH Categories

Habitats	***DBH Categories (cm)***				
	Small 20-70	***Medium 71-120***	***Large 121-200***	***Very Lg. >201***	***Total N***
Borokotò, N (%)	148 (69.15)	49 (22.89)	11 (5.14)	6 (2.80)	214
Capoeira, N (%)	151 (79.47)	27 (14.21)	11 (5.78)	1 (0.52)	190
Terra Firme, N (%)	189 (78.42)	41 (17.01)	10 (4.14)	1 (0.41)	241
All Non-Flooded Forest combined, N (%)	489 (75.81)	117 (18.13)	31 (4.80)	8 (1.24)	645
All igapó, N (%)	970 (68.50)	368 (25.98)	71 (5.01)	7 (0.49)	1416

Appendix III-2 lists the number of species per family for each habitat. Fig. III-2 summarizes this information, graphing the combined frequency distribution of species

per family for all igapó and with borokotò, capoeira and terra firme combined as 'non-igapó', showing over one-third of igapó plant families are represented by a single species.

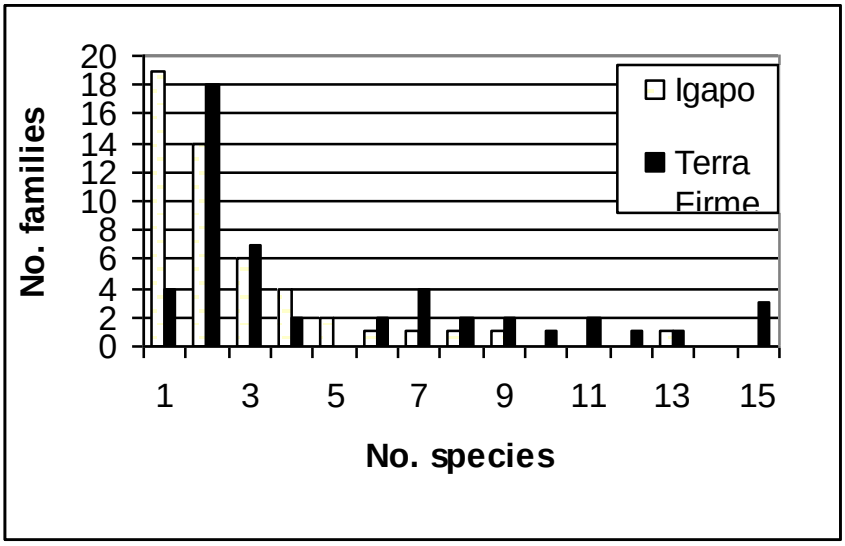


Fig. III-2: No. Species* per *Plant Family in Igapó and Terra Firme Forests

Fig. III-3 shows distribution frequency for the number of individuals *per* species, for igapó and for non-igapó (the non-flooded forest types, terra firme + borokotò + capoeira).

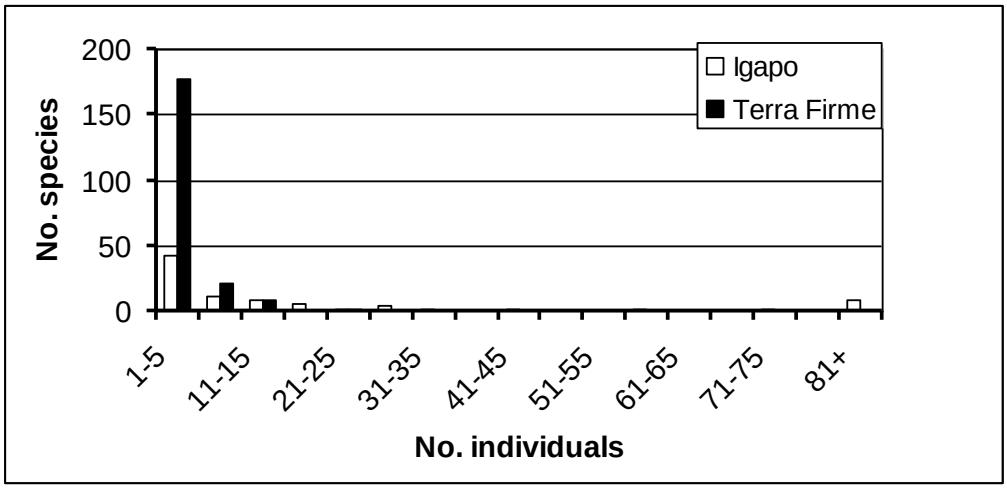


Fig. III-3: No. of Individuals* per *Species in Igapó and Terra Firme Forests

The levels of similarity between the habitats and sub-habitats was calculated using Jaccard Similarity Indices (Jaccard, 1901). These indices are used for comparing the

similarity and diversity of samples by measuring how many species of the pooled species set occur only in each individual sample, and how many are shared. It is a simple measure that does not take account of the proportions of the various species in the respective community, focusing instead simply on the presence or absence of the various species. Each Index is a pair-wise comparison of two samples and is calculated with the

$$J = \frac{A}{A + B + C}$$

Where: A = no. species in both samples,
B = no. species unique to sample 1
C = no. species unique to sample 2

This index has been widely used to compare species compositions of communities as diverse as invertebrates in soft marine sediments (e.g. Turner *et al.*, 1995), and bats in tropical rainforest (e.g. Barnett *et al.*, 2006). Values above .20 indicate high similarity between the samples. Table III-5 provides Jaccard values when comparing the species composition of the igapó quadrats, while Table III-6 does this between terra firme quadrats, and between terra firme habitats and all the igapó quadrats combined.

Table III-5: Jaccard Similarity Indexes between Igapó Quadrats

Q3	1				
Q7	0.224	1			
Q8	0.300	0.236	1		
PG1	0.220	0.212	0.134	1	
PG2	0.233	0.224	0.191	0.403	1
	Q3	***Q7***	***Q8***	***PG1***	***PG2***

Table III-6: Jaccard Similarity Indexes for the Three Non-floodedHabitats and All-igapó

All-Igapó	1			
Terra Firme	0.021	1		
Capoeira	0.016	0.081	1	
Borokotò	0.049	0.157	0.088	1
	All-Igapó	***Terra Firme***	***Capoeira***	***Borokotò***

Table III-7 shows the species diversity of each habitat for the following values: Shannon-Wiener Diversity Index (*H′*), Species Richness (S), Total Abundance, Simpson Diversity Index (1-D²) and Eveness. Because it measures both evenness and diversity, *H′* is considered to be an especially appropriate estimator of rainforest biodiversity (Stocker *et al.*, 1985).

Shannon-Wiener *H′* was calculated with the formula: $H = - \Sigma (P_i \log [P_i])$.

Simpson D was calculated with the formula: $D = \Sigma(p_i^2)$

Evenness was calculated with the formula: $E = H / \log(S)$

For the two igapó margin quadrats (PG1 and 2), where data was combined, for all others, data are given separately for each individual quadrat. Data are also combined to compare 'igapó interior' (quadrats 3, 7, 8) with the igapó margin community sampled by quadrats PG1 and 2, and for the three non-flooded habitats (borokotò, capoeira and terra firme: quadrats 4, 5, 6) to provide diversity measurements for 'all-TRF'.

Table III-7: Diversity Indices for the Sampled Habitats and Sub-habitats

	Species Richness	***Abun-dance***	***Shannon-Wiener (H')***	***Simpson D***	***Simpson 1-D***	***Simpson 1/D***	***Evenness***
Least-flooded Igapó (Q3)	26	361	2.219	0.082	0.822	5.781	0.681
Medium-flooded Igapó (Q7)	34	276	2.678	0.135	0.917	7.404	0.759
Longest-flooded Igapó (Q8)	13	305	1.925	0.200	0.800	4.994	0.750
Igapó margin (PG1 & PG2)	67	474	3.613	0.038	0.949	26.216	0.859
Igapó interior (Q3, Q7, Q8)	50	942	2.896	0.083	0.846	11.931	0.740
All Igapó	84	1416	3.442	0.054	0.872	18.287	0.776
Borokotò-Q4	107	214	4.388	0.016	0.983	58.962	0.939
Capoeira-Q5	48	190	3.492	0.037	0.962	26.505	0.902
Terra firme-Q6	114	241	4.386	0.018	0.981	53.042	0.926
All TRF	205	645	4.919	0.010	0.989	98.425	0.924

With exception of Simpson 1-D values for igapó, all index values calculated using diversity calculator at: http://www.changbioscience.com/genetics/shannon.html

3.3 Representativeness of Samples

Figs. III-4 to 7 graph, respectively, species accumulation curves for igapó (quadrat 3), borokotò (quadrat 4), capoeira (quadrat 5), and terra firme (quadrat 6). Fig. III-7 includes data from the two additional blocks that, as mentioned in Section 2.6.1, were included specifically to assess species accumulation rates in the highly species-diverse terra firme. Fig. III-8 gives species accumulation rates for PG1 and PG2, the two elongated transects that sampled the highly distinctive marginal igapó sub-habitats (Appendix III-1, Table III-5, images in Chapter 2). In each case, the plot is of the number of new species added with each sequential 10x25m block of the quadrat. For each, the plot represents the number of species added by sequential 10x25m blocks of a 10-block quadrat. In each sample, the resulting curve heads for an asymptote by the time the tenth block is reached, indicating a sample that is nearing representative completion.

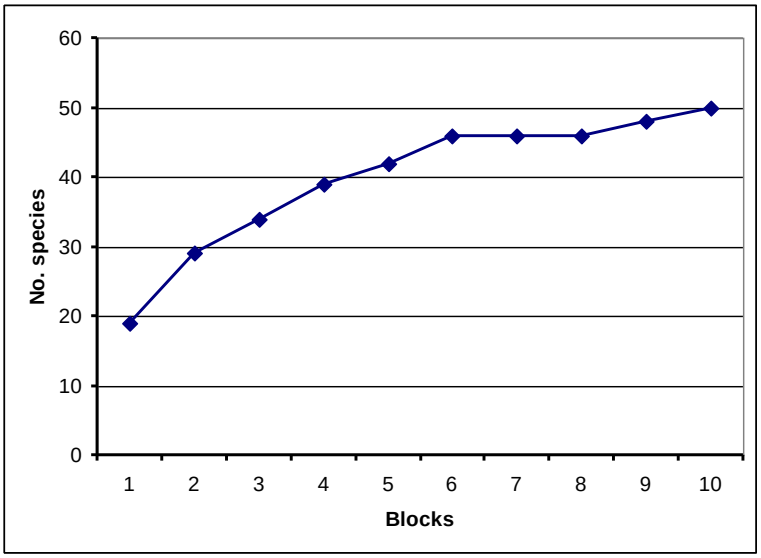


Fig. III-4: Tree Species Accumulation Curve for Sampled Igapó (Q3)

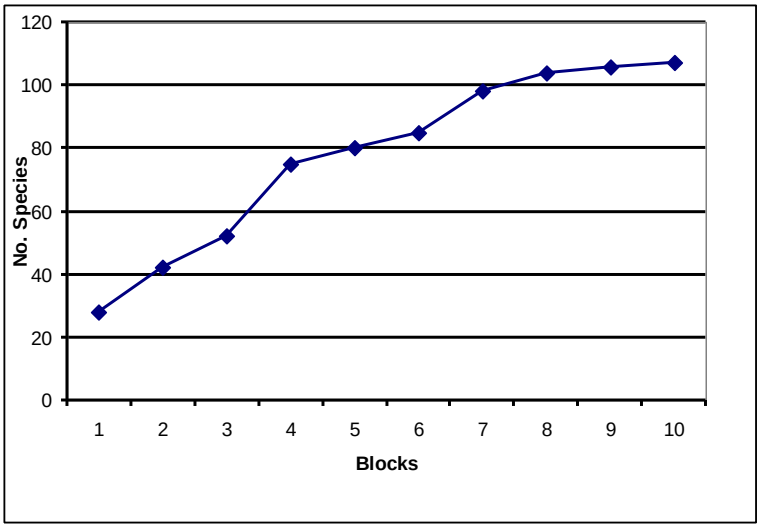


Fig. III-5: Tree Species Accumulation Curve for Sampled Borokotò (Q4)

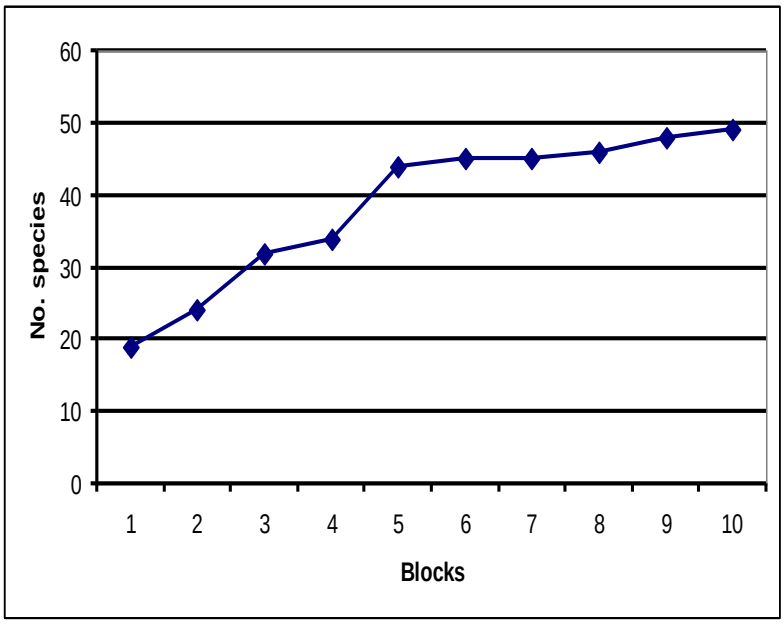


Fig. III-6: Tree Species Accumulation Curve for Sampled Capoeira (Q5)

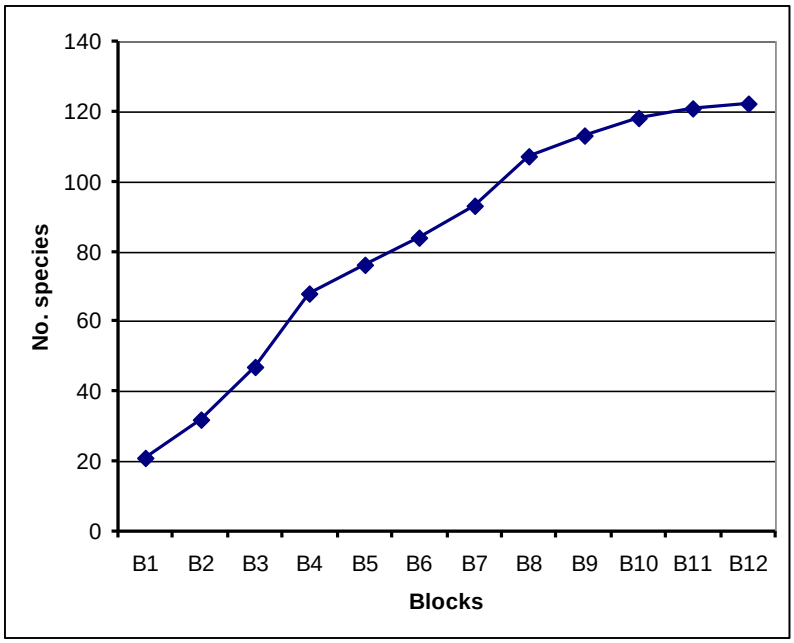


Fig. III-7: Tree Species Accumulation Curve for Sampled Terra Firme (Q6)

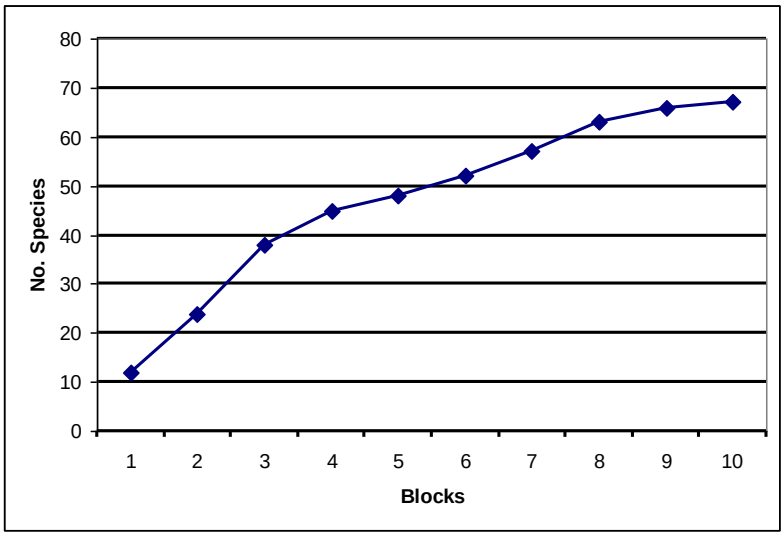


Fig. III-8: Tree Species Accumulation Curve for Sampled River Margin Igapó (PG1 and PG2)

Estimations of sample completeness used the linear dependence model (Moreno & Halffter, 2000): and the equation S(t) = a/b [1- exp (-bt)] to estimate the total number of species in an area from which the sample had been drawn. Where:

t = measure of effort (here no. of quadrats)

S = predicted total no. species

a = rate of increase at the beginning of the sampling

b = species accumulation

and exp is a constant (2.7128).

Results are given in Table III-8.

Table III-8: Estimated Completeness of Sampled Quadrats

Quadrat	*Habitat*	*Estimated Max. No.*	*% Estimated Completeness*
3	*Least-flooded Igapó*	*60*	83.3
4	*Borokotò*	*111*	96.3
5	*Capoeira*	*54*	90.7
6	*Terra firme*	*129*	89.9
7	*Medium-flooded Igapó*	*42*	80.9
8	*Longest-flooded Igapó*	*38*	71.0
PG1 & PG2	*River Margin Igapó*	*74*	81.9
Mean Completeness			*86.0*

3.4 Phenology

Fig. III-9 shows the monthly distribution of the number of species bearing fruit, in igapó, borokotò and terra firme. Fig. III-10 shows this with data for phenotrails added. Figure III-11 also includes data from phenotrails, but adds data for monthly production of new leaves, and presents these data as ‘flooded’ (igapó) and ‘non-flooded’ (terra firme + borokotò) habitats. Where no data were collected, the missing values are indicated with a gap. The data set for capoeira (an area of regenerating terra firme) was incomplete and was therefore not included in the phenological analysis.

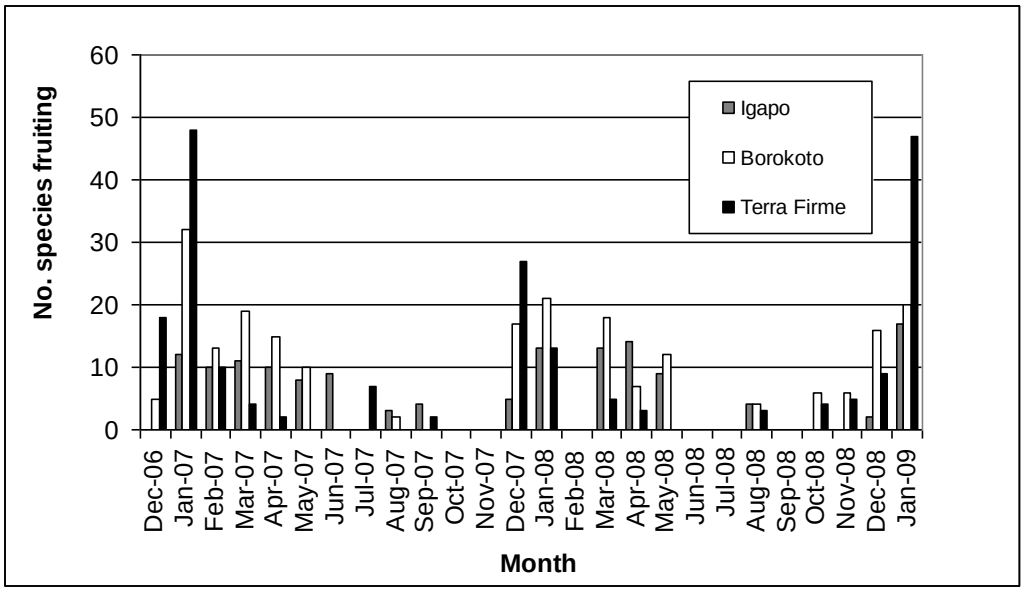


Fig. III-9: Number of Tree Species Fruiting Monthly in Three Habitats, Dec 2006 - Dec 2008, Quadrat Data Only

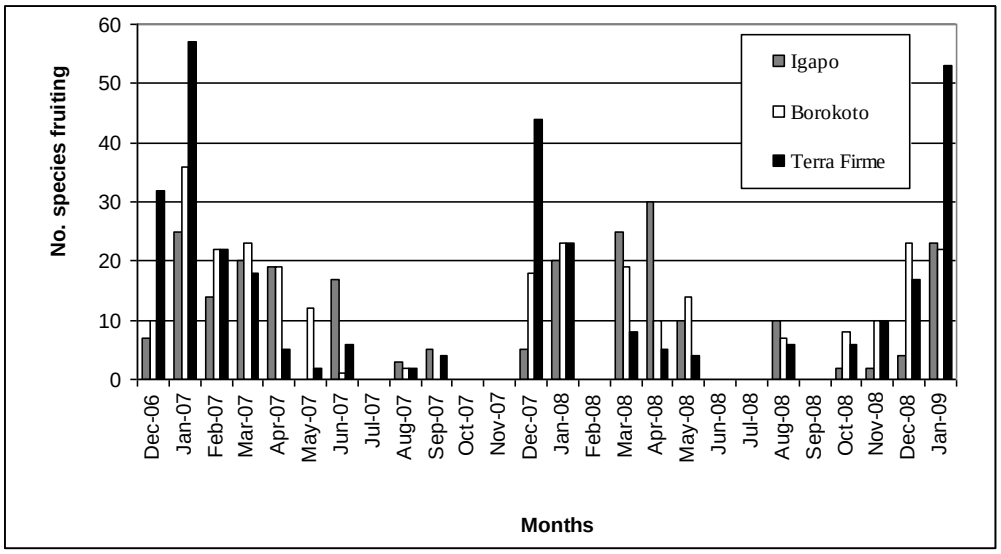


Fig. III-10: Number of Tree Species Fruiting Monthly for Three Habitat Types, Quadrats, plus Phenotrails (Dec 06-Apr08)

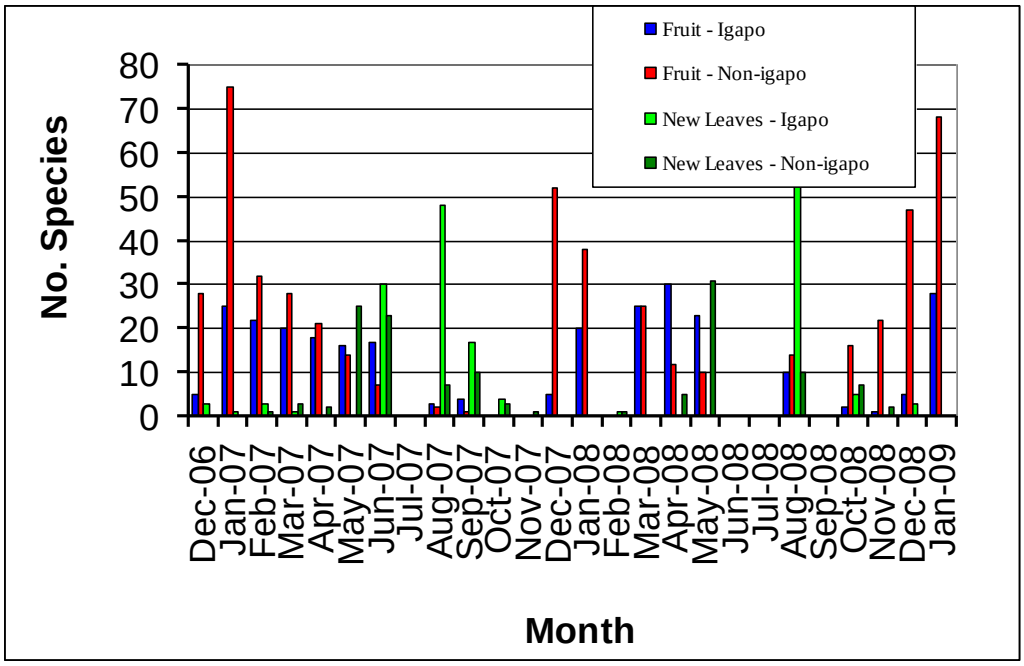


Fig. III-11: Monthly No. Tree Species Fruiting and Producing New Leaves

A notable difference exists in leaf production between the two habitats. In igapó 82% of new leaf records (individuals), and 79% of leaf-flush activity (by species) occurs between the months of Jun and Sep. In terra firme, leaf flush is a broader event with net leaf flushing being concentrated during the dry season (Jul-Oct: Fig. II-1).

3.5 Crop Volume

Tables III-9 and III-10 present mean fruit crop volumes for tree species from, respectively, igapó and terra firme habitats. These have been calculated by direct measurement of specimen trees (Section 2.7.1). CVEM refers to 'Crop Volume Estimation Method' given in Table II-5. The species selected were either known uacari diet species, was one of the ten most common trees in the habitat in question, or both. Crop volume estimates were not made for palms, nor for lianas.

Table III-9: Mean Fruit and Seed Crop Volumes for Selected Igapó Tree Species

Species	***N***	***CVEM***	***Mean canopy volume (m^3) (SD)***	***Mean no. fruit per tree (SD)***	***Mean no. fruit per m^2 canopy***	***Mean fruit weight (g) (SD)***	***Mean fruit weight (g) per m^2 canopy***	***Mean total seed weight per fruit (g) (SD)***	***Mean total seed weight (g) per m^2 canopy***	***Mean fruit/ seed weight (g) for entire mean canopy***
Aldina heterophylla	6	II: Direct sub-sample	169.61 (172.91)	256 (166.53)	1.5	298.33 (109.89)	447.49	281.71 (107.61)	442.56	75,898 75,062
Amanoa oblongifolia	7	V: Cluster count	53.9 (28.94)	309.75 (231.01)	5.7	2.18 (1.07)	12.42	1.065 (0.072)	6.07	669.43 327.17
Buchenavia ochrograma	6	II: Direct sub-sample	53.74 (33.06)	209.83 (167.68)	3.9	1.375 (0.11)	5.36	0.724 (0.102)	2.82	288.04 151.54
Casearia sp.	6	II: Direct sub-sample	39.21 (16.56)	87.66 (65.72)	2.23	1.78 (0.39)	3.96	0.78 (0.30	1.74	155.27 68.22
Chaunochiton loranthoides	6	II: Direct sub-sample	47.19 (20.41)	241 (179.94)	5.1	1.57 (0.62)	8	1.175 (0.38)	5.99	377.52 282.66
Crudia amazonica	5	I: Direct total counting	60.6 (8.71)	227.4 (107.21)	3.75	85.88 (25.92)	332.05	76.2 (24.6)	285.75	20,122.2 17,316.5
Duroia velutina	6	III: Coll. from branches	43.43 (19.48)	106.16 (89.29)	2.44	21.98 (8.85)	53.63	16.62 (7.87)	40.55	2,329.15 1,761.08
Eleoluma glabrescens	6	II: Direct sub-sample	100.09 (14.44)	304.83 (201.79)	3.04	2.23 (0.47)	6.78	1.22 (0.42)	3.7	684.1 373.33
Eschweilera tenuifolia	12	II: Direct sub-sample	103.85 (44.12)	33.75 (26.48)	0.33	169.23 (48.68)	55.84	88.08 (30.93)	29.04	5,798.98 3,015.8
Licania heteromorpha	6	II: Direct sub-sample	108.19 (43.25)	145.33 (134.47)	1.34	7.75 (0.32)	10.38	6.06 (0.23)	8.12	1,123.01 878.5
Mabea nitida	8	V: Cluster count	79.77 (22.99)	265 (207.54)	3.32	2.18 (1.07)	7.23	1.065 (0.072)	3.53	576.73 281.58
Macrolobium acaciifolium	17	II: Direct sub-sample	135.33 (46.83)	210 (182.81)	1.55	9.36 (2.63)	14.5	5.09 (1.72)	7.88	1,962.28 1,066.4
Micropholis venusta	8	IV: Total tree count	81.74 (26.74)	257.37 (218.86)	3.14	5.0 (1.08)	15.7	3.64 (0.75)	11.42	1,283.3 933.47
Mouriri sp.	4	II: Direct sub-sample	22.19 (9.66)	55 (39.26)	2.47	13.7 (9.0)	33.84	1.25 (0.17)	3.08	750.90 68.34
Myrtaceae (*Eugenia* sp.)	4	V: Cluster count	9.81 (3.94)	106.25 (50.76)	10.83	0.62 (0.31)	6.71	0.32 (0.13)	3.2	65.82 31.39
Pouteria elegans	6	IV Total tree count	151.31 (110.73)	206.16 (253.35)	1.36	3.45 (1.6)	4.7	2.7 (1.3)	3.67	711.15 555.3

Table III-9: Mean Fruit and Seed Crop Volumes (contd) – 1

Species	*N*	*CVEM*	*Mean canopy volume (m^3)* *(SD)*	*Mean no. fruit per tree* *(SD)*	*Mean no. fruit per m^2 canopy*	*Mean fruit weight (g)* *(SD)*	*Mean fruit weight (g) per m^2 canopy*	*Mean total seed weight per fruit (g)* *(SD)*	*Mean total seed weight (g) per m^2 canopy*	*Mean fruit/ seed weight (g) for entire mean canopy*
Pouteria elegans	6	IV Total tree count	151.31 (110.73)	206.16 (253.35)	1.36	3.45 (1.6)	4.7	2.7 (1.3)	3.67	711.15 555.3
Swartzia laevicarpa	5	I: Direct total counting	38.09 (14.43)	43.6 (21.99)	1.14	11.25 (2.32)	12.82	7.9 (1.51)	9	488.3 342.81
Swartzia acuminata	6	I: Direct total counting	124.5 (62.92)	126 (79.03)	1.01	247.22 (95.07)	249.7	105 (86.88)	106.05	31,087.6 13,203.2
Ternstroemia candolleana	5	III: Coll. from branches	28.81 (8.84)	98.8 (60.67)	3.42	0.73 (0.22)	2.5	0.59 (0.22)	2.01	72.02 57.9

Note: the crop volume value for Licania heteromorpha *was for fruit pulp, not seed, as uacari ate pulp only from this species.*

Table III-10: Mean Fruit and Seed Crop Volumes for Selected Terra Firme Tree Species

Species	***N***	***CVEM***	***Mean canopy volume (m^3)*** ***(SD)***	***Mean no. fruit per tree*** ***(SD)***	***Mean no. fruit per m^2 canopy***	***Mean fruit weight (g)*** ***(SD)***	***Mean fruit weight (g) per m^2 canopy***	***Mean total seed weight per fruit (g)*** ***(SD)***	***Mean total seed weight (g) per m^2 canopy***	***Mean fruit/ seed weight (g) for entire mean canopy***
Bellucia grossularioides	5	II: Direct sub-sample	39.06 (17.72)	364 (81.06)	9.31	6.4	59.58	2.9	26.99	2,327.2 1,054.2
Bombacopsis sp.	1	I: Direct total counting	100.48	174	1.73	66	114.18	17	29.41	11,472.8 2,955.1
Chrysophyllum sanguinolentum	4	II: Direct sub-sample	91.56 (19.93)	127.5 (64.24)	1.39	16.42 (3.63)	22.82	9.77 (3.11)	13.58	2,089.4 1,243.4
Diospyros manuensis	4	II: Direct sub-sample	24.72 (5.42)	160 (140.71)	6.47	2.65 (1.03)	17.14	1.53 (0.24)	9.9	423.7 244.7
Eschweilera truncata	4	II: Direct sub-sample	23.76 (19.24)	43.75 (19.65)	1.84	14.8	27.23	6.4	11.78	647.98 279.89
Inga obidensis	6	II: Direct sub-sample	49.68 (15.61)	273 (146.09)	5.49	17.7	97.17	14.8	81.25	4,827.4 4,036.5

Table III-10: Mean Fruit and Seed Crop Volumes, Terra Firme (contd.) – 1

Species	*N*	*CVEM*	*Mean canopy volume (m^3)* *(SD)*	*Mean no. fruit per tree* *(SD)*	*Mean no. fruit per m^2 canopy*	*Mean fruit weight (g)* *(SD)*	*Mean fruit weight (g) per m^2 canopy*	*Mean total seed weight per fruit (g)* *(SD)*	*Mean total seed weight (g) per m^2 canopy*	*Mean fruit/ seed weight (g) for entire mean canopy*
Licania oblongifolia	3	II: Direct sub-sample	66.16 (49.18)	252 (94.29)	3.8	6.27	23.82	4.73	17.97	1,575.93 1,188.89
Miconia poeppeigii	5	III: Coll. from branches	39.84 (20.73)	791.6 (277.98)	19.86	0.47	9.33	0.43	8.53	371.70 339.84
Protium sp.	4	V: Cluster count	29.65	126.75 (83.57)	4.27	3.7	15.79	2.4	10.24	468.2 303.61

Note: *Licania oblongifolia* values are for the pulp, to provide comparability with *L. hereromorpha* in igapó

Fig. III-12 shows the distribution of number of individual trees, palms and lianas in DBH in 10cm size classes across from quadrats in flooded (igapó) and non-flooded habitats (borokotò, capoeira and terra firme combined).

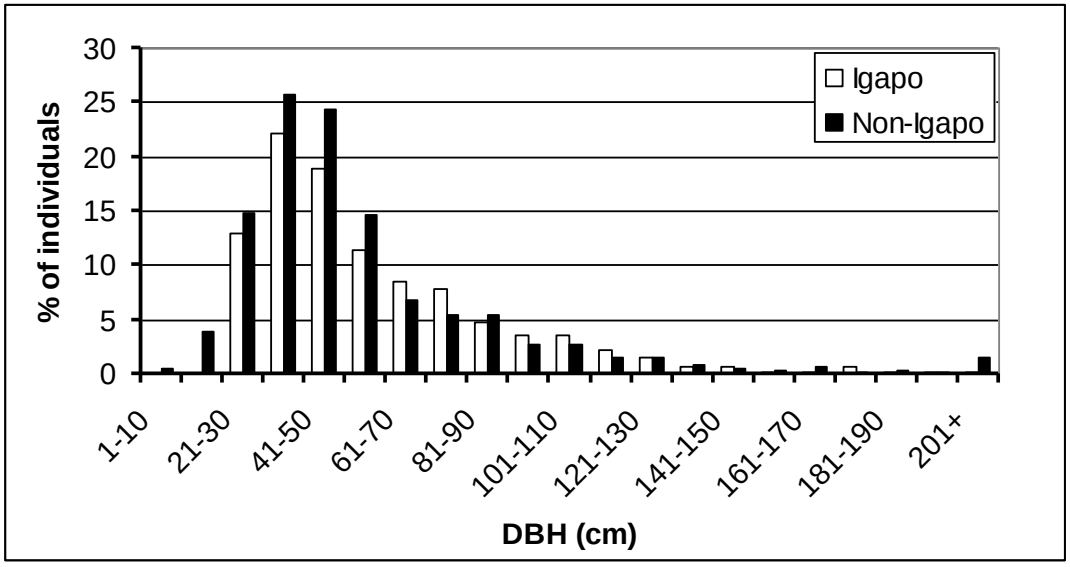


Fig. III-12: DBH Distribution for Individual Trees, Palms and Lianas from Igapó and Non- igapó Habitats.

Crop volumes were calculated for flowers of selected species (Section 2.7.2). Table III-11 gives number of simultaneously open flowers on individual trees of *Eschweilera*

tenuifolia (Lecythidaceae) in 2007/8 and 2008/9 flowering seasons. Table III-12 gives the number of flowers on 23 *Codonanthe crassifolia* vines, and the size of each vine.

Table III-11: Number of Simultaneously Open Flowers on Individual* Eschweilera tenuifolia *Trees

Tree no.	*DBH*	*Canopy (LxH)*	*Canopy curved surface area, m² (2πr²)*	*Inflorescence no. in 2008 and 2009*	*No. open flowers, 2008/9*	*No.open flowers/m² canopy, 2008/9*
1	114	3.5, 1.5	19.23	46/13	92/26	4.8/1.35
2	78	2.8, 2.5	12.31	5/--	10/--	0.8/--
3	75	2.6, 1.8	10.61	29/5	58/10	5.5/0.9
4	86	3, 2.8	14.13	38/--	76/--	5.4/--
5	48	1.8, 2.1	05.09	17/2	34/4	6.7/0.8
6	66	2.6, 2	10.61	31/8	62/16	5.8/1.5
7	53	2.7, 2.1	11.45	28/--	56/--	4.9/--
8	101	4.1, 3.2	26.39	47/8	94/16	3.6/0.6
9	94	3.5, 2.8	19.23	37/5	74/10	3.8/0.5
10	57	2.4, 1.8	09.04	2/19	4/38	0.4/4.2
11	68	2.7, 2	13.25	31/6	62/12	4.7/0.9
12	81	2.7, 2.2	13.25	34/7	68/14	5.1/1.1
13	74	3.1, 1.4	15.09	32/3	64/6	4.2/0.4
14	86	2.8, 2.2	12.31	24/2	48/4	3.9/0.3
15	105	3.8, 2.4	21.67	53/7	106/14	4.9/0.6

Note: The canopy of Tree 2 was partially destroyed by a tree fall in Mar 2008. Tree 4 died between 2008 and 2009. Tree 7 was lost.

Table III-12: Number of Simultaneously Open Flowers on Individual* Codonanthe crassifolia *Vines

Vine No.	*Patch size (cm²)*	*No. open flowers*	*Vine No.*	*Patch size (cm²)*	*No. open flowers*
1	183	17	**13**	72	16
2	86	11	**14**	173	6
3	64	5	**15**	124	5
4	91	9	**16**	33	6
5	73	0	**17**	68	7
6	68	17	**18**	212	33
7	82	2	**19**	49	9
8	190	7	**20**	117	36
9	54	9	**21**	48	0
10	58	17	**22**	66	14
11	109	16	**23**	85	9
12	82	0	**Means**	*95 08cm² SD±49.58*	*10.91 SD±9.26*

3.6 Discussion

As they depend on plants for food and shelter, the ecology of a primate population is intimately tied to the composition of the plant community it inhabits. Variations in phenology, abundance, nutrient composition and predictability of foods can have profound effects on the timing of reproduction, sizes of groups and the social structure within them (Boubli, 2005; Brockman & van Schaik, 2005), and hence knowledge about them is profoundly important for the formulation of effective conservation strategies (Cowlishaw & Dunbar, 2000).

3.6.1 Plant Community Composition

Number of Species: The number of species in each study habitat appears to accord with those of other studies of botanical species diversity in Amazonia and associated Neotropical lowland forests, as do the measures of species diversity (Table III-13).

Table III-13: Number of Tree Species and Shannon-Wiener Diversity Indices from other Neotropical Rainforest Areas

Habitat	***Locality***	***No. tree species***	***Shannon-Wiener****	***Author***
Igapó	***Jaú National Park, Central Amazonas, Brazil***	***89***	***3.32***	***Current study***
Várzea flooded forest	Central Amazonia, Brazil	109, 135	1.82, 1.93	Ayres (1986a)
Várzea flooded forest	Northern Amazonian Peru	142	--	Bowler (2007)
Várzea flooded forest	Central Amazonia, Brazil	74	3.60, 3.51, 1.82	Campbell *et al.* (1992)
Várzea flooded forest	Northern Amazonian Peru (Tambopata)	155	--	Gentry (1988)
Igapó	Bolivia	72	3.55	Mostacedo *et al.* (2006)
Igapó	Vaupés State, eastern Colombian Amazon	112	--	Schütz (2008)
Non-flooded rainforest	***Jaú National Park, Central Amazonas, Brazil***	***212***	***4.94***	***Current study***
Lowland Amazonian rainforest	Northern Amazonian Peru (Río Yavarí)	199	--	Bowler (2007)

Table III-13: Comparative Diversity Indices from other Neotropical Rainforest Areas (contd.) - 1

Habitat	*Locality*	*No. tree species*	*Shannon-Weiner**	*Author*
Lowland Amazonian rainforest	North-west Amazonia, Brazil (Base, Pico de Neblina)	102	--	Gentry (1988)
Lowland Amazonian rainforest	Northern Amazonian Peru (Cabeza de Mono)	185	--	Gentry (1988)
Lowland Amazonian rainforest	Northern Amazonian Peru (Cocha Cashu)	204	--	Gentry (1988)
Lowland Amazonian rainforest	Northern Amazonian Peru (Mishana)	289	--	Gentry (1988)
Lowland Amazonian rainforest	Northern Amazonian Peru (Tambopata)	181	--	Gentry (1988)
Lowland Amazonian rainforest	Northern Amazonian Peru Yanomono)	300	--	Gentry (1988)
Seasonally dry Amazonian forest	Roraima State, northern Brazil	80	--	Milliken & Ratter (1998)
Lowland Amazonian rainforest	Bolivian Amazon	200	3.8	Mostacedo *et al.* (2006)
Lowland Amazonian rainforest	Central Amazonas State, Brazil	201	--	Milliken (1998)
Primary lowland rainforest,	Pará State, eastern Amazonia, Brazil	148	6.69	Pinto (2008)
Old secondary lowland rainforest	Eastern Amazonia, Brazil	259	4.07	Santana *et al.* (2004)
Lowland rainforest	Atlantic coast, Brazil	263	4.07	Sanchez *et al.* (1999)
Lowland rainforest (Colinas)	Vaupés State, eastern Colombian Amazon	256	--	Schütz (2008)

* Note 1: values are calculated in Log base 2.

In a broad Amazonian context, the species diversity of forests at Jaú appear to be unexceptional, according (for igapó) with its habitat type, and (for terra firme) with its geographical position. The species diversity of igapó has been found to be lower than that of várzea, and though the higher nutrient throughput of the várzea system may be partly responsible for this (Boubli, 2005), the complexity of the levée-and-slough topography is also considered influential (Ayres, 1983), as is the sheer size of the floodplain in comparison to the narrow ribbons of igapó (Fereira *et al*., 2005). The key variables in determining species abundance in terra firme forest is the west-east gradient of soil

fertility and rainfall intensity and rainy season duration (Pitman *et al*., 2001; ter Steege *et al*., 2003), though historical factors and the presence of the lower montane Andean flora in the west are also important (Colinveaux, 2007; Haffer, 2008).

Proportions of species

As Hill (1973) originally recognized, evenness is an important value in community ecology, since it measures the proportional contribution of a community's component species to the total number of individuals in the community. That is, a community of 10 species where each species has the same number of individuals is considered to be more equal (more even) than one in which one or a few species have numerical prominence.

By this criterion, the sampled terra firme at Jaú was highly diverse, with 97 (65.9%) of the 147 species were represented by a single individual (Appendix III-1 and Figure III-3). That borokotò was the most species-diverse of all habitats (127 species) is most likely due to the diversity-enhancing effect of topographical variation provided by the hummocks, permitting the close spatial coexistence of species with differing tolerance for various soil conditions and inundation durations. In borokotò, capoira and terra firme combined no single species contributed more than 4% of the 645 registered individual trees, palms and lianas. *Gustavia elliptica* (Lecythidaceae) was the most common species, with 21 individuals, or 3.25% of the total. In these three non-flooded quadrats combined, the most numerous six species (*G. elliptica*; *Protium trifoliatum*: Burseraceae, N=14; *Aniba ferrea*, Lauraceae N=13; *Swartzia* sp., Fab. Pap., N=13; *Tapirara obtuse*: Anacardiaceae, N=13; *Virola mollisima*: Myristicaceae, N=13) together constituted barely one-eighth (13.48%) of the total number of individual trees (N=87: Table III-2).

In igapó, by contrast, the most numerous six species (*Amanoa oblongifolia*: Euphorbiaceae, N=150; *Pouteria elegans*: Sapotaceae, N=146; *Eschweilera tenuifolia*: Lecythidaceae, N=137; *Buchevania ochrogramma*: Combretaceae, N=94; *Eleoloma glabrescens*: Sapotaceae, N=92 and *Mabea nitida*, Euphorbiaceae, N=75); and) together constituted almost half (49.01%) of the 1416 individual trees registered across all igapó quadrats (N=694: Table III-1). Thus, though it is a species-rich habitat, igapó has lower evenness and lower community diversity than the terra firme (Table III-7). This has potential consequences for the foraging ecology of the golden-backed uacari.

As may be seen in Table III-1, the species composition of the igapó forest was highly skewed, with the six most abundant species contributing between 61 and 88% of the individuals in the sample quadrat. The exception is the species-rich and high-evenness habitats (Table III-7) at the igapó margin, where it does not exceed 39%. In contrast, the terra firme community possessed more evenness, the six most abundant species together contributing no more than 36% of the species total in any of the non-flooded quadrats (Table III-2), and not more than 14% overall.

Consistent with the flood-tolerant-based banding that structures igapó plant communities (Ferreira, 1997, 2000), each of the igapó quadrats was dominated by a different set of species. These corresponded to progressively more flood-tolerant species in the following quadrat sequence Q3>Q7>Q8>PG1&PG2. The marginal habitat sampled by PG1 and 2 is far more species-rich/individual-poor than the rest of the igapó. This presence of highest diversity in the most biologically challenging sub-habitats accords with Silvertown's dynamic equilibrium model of plant community diversity, which proposes that the most species-rich habitats will be the ones where an

environment that is either permanently inimical (e.g. nutrient poverty or anoxia) or which suffers frequent but unpredictable perturbation, preventing the establishment of any one species or suite of species from attaining dominance (Silvertown, 2008). In the case of the river margins, these conditions are met because the community will have the longest periods of inundation and are the most scoured and disrupted by river action. The combination of the two may well act synergistically, augmenting diversity above those levels experienced in the non-margin igapó areas. Small trees (DBH ≤ 30cm) was also less common in the terra firme quadrat than in the PG1 and PG2 quadrats (10.7% *vs.* 14.19%, PG data combined). In addition, isolation-rich areas such as margins and gaps are frequently populated by sun-tolerant plant species, which have faster growth and maturation rates than shade-tolerant conspecifics (e.g. Bazzaz & Pickett, 1980; Chazdon & Field 1987). Combined, these factors not only allow a higher density of individual plants (479 in PG quadrats *vs*. 327 in terra firme), but may also have meant a higher propoprtion of species with life-strategies at the *r* end of the *r*/*K* continuum (MacArthur & Wilson, 1967; Southwood, 1988; Southwood *et al*., 1977), so that reproductive adults will appear more rapidly after a perturbation (Grime, 2001; McNeely, 1994).

Igapó has a lower level of evenness than terra firme. As it is more likely there than in terra firme that the next tree encountered will be one that is a fruiting tree of the kind currently being used by the uacari as part of its diet., this means that, in terms of resource availability, igapó is likely to be more homogeneous, and hence possibly more reliable as a source of food for foraging uacaris. As will be seen in Chapters 4 and 5 and 6, this has consequences for uacari diet choice, time budget and group size.

Comparison of DBHs in Table III-4 shows the distribution of trees in the four size categories is very similar across habitats, with in all cases the majority of plants (between 67.3 and 79.4%) being in the 20-70cm DBH category. These are not, therefore especially large trees. In igapó this may be due to the adverse nature of the physical environment, which requires a suite of physiological specializations (de Simone *et al.*, 2002, 2003; Lobo & Joly, 1998), and results in generally slow tree growth rates (da Fonseca Júnior *et al.*, 2009; Schöngart *et al.*, 2002; Worbes, 1989).

Species composition profiles given in Tables III-1 and III-2 reveal the a dominance in terra firme of Burseraceae, Euphorbiaceae, Fabaceae, Lecythidaceae and Sapotaceae that is very characteristic of the central Amazonian forests (Gentry, 1991; Santana *et al.*, 2004; Milliken, 1998). The family Chrysobalenaceae had a remarkable richness (15 species) of *Licania* in the sampled terra firme forest. In Amazonia, both the Annonaceae and Myrtaceae are very diverse families, but both are dominated by small understory treelets which generally only just reach the minimum DBH category of 20cm (Gaeverts *et al.*, 2008; Maas, 1989; Ribeiro *et al.*, 1999). The dominance of Fabaceae and Sapotaceae in igapó has been noted by other authors (e.g. Ferreira & Stohlgren, 1999; Worbes, 1997), and may reflect physiological specializations concomitant with nitrogen-fixing bacteria (Fabaceae: Crews, 2005), and mychorrhizal associations (Sapotaceae: Lobo & Joly, 1998; de Simone *et al*., 2003).

As Figure III-3 shows, the number of species represented by a single individual was very much higher in non-flooded than flooded habitats. For uacaris this has important consequences for the spatial dispersion as well as its temporal predictability, and both of these factors have strong influences on search times and hence on activity budgets

(Chapter 4), habitat choice (Chapter 4), and diet item choice (Chapter 5).

The patterns of botanical similarity between habitats

Compositional similarity between flooded and non-flooded plant communities at Jaú is very low – with only one species in common between interior flooded forest and never-flooded primary lowland forest (terra firme). This is because igapó plants are highly specialized: not only do they grow on extremely poor soils (Furch, 1997), but must also endure many months of inundation (Ferreira, 1997). The suite of adaptations required for physiological tolerance of extended inundation include resilience to anoxic soil conditions (which itself includes a suite of circumstances including low oxygen concentrations, high soil pH and redox potential, and the presence of anaerobic microorganisms and their metabolic byproducts [hydrogen sulphide, alchohols, methane, phenolics and volatile fatty acids], all at potentially toxic levels: Ponnamperuma, 1984), low dissolved oxygen availability to roots (Arruda & Calbo, 2004) and, for completely inundated species, the reduction of available oxygen and light to leaves (Parolin *et al.*, 2004b; Schlüter *et al.*, 1993). Even if the individual plant is large enough not be submerged completely, flooding still imposes substantial stresses on igapó trees (Parolin, 2000b; de Simone *et al.*, 2002, 2003), and such plants have many morphological and behavioural adaptations in addition to their physiological ones (Worbes, 1985).

The specializations involved in living in igapó have resulted in some species evolving physiologically specialized sub-populations whose members cannot successfully germinate in the others' environment (e.g. C. Ferreira *et al.*, 2005 for *Himatanthus sucuuba*: Apocynaceae), while others (e.g. *Pentaclethra macroloba*: Fab.: Mim.) have populations of igapó-living trees with floating seeds, and terra firme individuals which produce heavier non-floating seeds (Williamson & Costa, 2000). Other taxa are now fully

taxonomically-distinct sister species (Parolin *et al.*, 2004b).

The presence of sister species pairs of trees, one each in the adjacent igapó and terra firme habitats was recorded here in several genera, including *Eschweilera, Lachmellea* (Apocynaceae), *Mouriri* (Memyclaceae) and *Sclerolobium* (Fab.: Caes.). That, within families with igapó-inhabiting representatives, this specialization has occurred at the species- rather than generic-level is seen from the high Jaccard values in Table III-6. Of the 139 genera recorded, 25 were registered only in igapó and 61 only in terra firme. However, many of these were represented by single records, and hence sampling error cannot be excluded. When both single species records and records of genera represented by multiple species, each with a single record are excluded, then 17 genera are found only in igapó and 36 only in terra firme. Only *Licania* sp., *Maprouna guianensis* (Euphobiaceae), *Myrcia paivae* (Myrtaceae), *Sclerolobium* sp. (Fab.: Caes.), *Swartzia panacoco* (Fab.: Pap.), and *Virola* sp. (Myristicaeae) occurred in both igapó and the never flooded habitats of terra-firme and/or capoeira.

Compositional differences within the igapó habitat

Table III-5 indicates that there are moderate levels of difference between the igapó quadrats. These almost certainly reflect that fact that the quadrats were positioned at different distances from the bank and so are commensurate with the inundation-tolerance mediated banding effects reported by Ferreira (1997a; L. Ferreira *et al*., 2005). Analysis of data in Appendix III-1 also shows that 39 of the species in igapó are unique to the margin area sampled by PG1 and 2 combined (58.2% of species in these forest margin quadrats). Only two species occurred in all five sampled igapó quadrats (*Eleoluma glabrescens* and *Hydrochorea marginata*). Six species were shared by four of the five igapó quadrats (*Acosmium nitidens, Eschweilera tenuifolia, Mabea nitida, Ormosia*

paraensis, Macrolobium acaciifolium, Pouteria elegans). These eight species were among the commonest species in igapó (Table III-1), and also (Chapter 5) among the most frequently eaten.

Of the species in Quadrat 3, 62.9% (N=17) were identified by Ferreira (2000) as having the lowest inundation tolerance of any tree species within the igapó community. Contrastingly, those from quadrats 7 and 8 contain progressively more of the species designated by Ferreira (2000) as possessing the greatest tolerance to inundation. Igapó species vary greatly in physiological tolerance to duration of inundation (Joly & Crawford, 1982), and, unsurprisingly, the species on the igapó margin (quadrats PG1 and PG2) contain a high incidence of species known, from the work of Ferreira (1997a,b, 2000) and others, to be able to tolerate extended inundation and, in some cases, complete immersion (Parolin *et al*., 2004b).

Consequences for uacaris of differences in botanical composition between fooded and non-flooded habitats

Of the 2061 individual plants in the quadrats, 72 individuals were lianas or vines and 55 were palms. Capoeira, igapó, and terra firme were comparatively species poor for lianas (2, 3 and 4 species, respectively), whilst borokotò had 16 individual lianas from 9 species. De Castilho (2004) registered 33 palm species in Jaú, eight of these (*Astrocaryum jauari, A. aculeatum, Attalea maripa, Euterpe precatoria; Leopoldinia pulchra, Oeoncarpus bacaba, Orbignya speciosa, Socratea exorrhiza)* were recorded in the quadrats, and four more were recorded outside the quadrats: *Attalea attaleoides* in terra firme, *Bactris maraja* in igapó, *Mauritia flexuosa* and *M. huebneri* in the mixed buritízal stands in which they dominate. Both *A. jauari* and *L. pulchra* tend to form near-monodominant stands and be rare outside these (Kubitzki, 1991; Piedade *et al*., 2005).

This clumping has almost certainly led to sample underestimating the abundance of these plants in the habitat as a whole. This is also true of the tree *Duroia velutina* (Rubiaceae), which preferentially colonizes areas of igapó that have been burnt in the dry season (this occurs naturally when lighting strikes ignite accumulated leaf litter), and can also form extensive stands. In one area close to quadrat 8, *D. velutina* constituted 38 of 50 counted trees, but only 3 of the next 50 were of this species. Such clumping means that, while species accumulation curves may indicate that the sample is approaching unity, and the species list is nearly complete (Section 3.3), this does not mean that the proportions at which some of the species occur are accurately represented. This may affect the accuracy of choice ratios when diet selection is considered.

As might be expected in an area that was cultivated up to 15 years previously, the composition of capoeira was dominated by fast-growing species, many of which were either gap specialists or colonizers of disturbed land (e.g. *Cordia, Dipteryx, Inga* species). The presence of large individuals in the capoeira study quadrat is due to the fact that some were edible by humans (e.g. *Bertholletia, Euterpe*) and were probably remanants of cultivation. Others, providers of shade and wood, were left standing during the original clearance, and are therefore older than the other trees on the quadrat (Eduardo de Souza, pers. comm.). A similar mix in regenerating agricultural plots of tree species characteristic of undisturbed terra firme and of secondary forest and tree-fall gaps has been recorded in Amazonian Colombia by Fujisaka *et al.* (1997).

Comparison of species compositions of the borokotò of Jaú and other localities is hampered by a lack of previously published studies on this habitat type (at least, under this name). However, the habitat may well be similar to the *bosque de tahuampa*

(floodplain forest) and *bosque de colina* (undulating terrain) recorded by Heymann *et al.* (2002) in Amazonian Peru. These are likewise habitats of alternating hillocks and small sloughs, which, like borokotò, have a high percentage of species from both igapó and terra firme (Kahn & Mejia, 1990; Kvist & Nebel, 2001; Nebel *et al.,* 2001).

Tables III-5 and 6 show that igapó and terra firme have very different species compositions. Indeed, with only 1 species in common (an *Eugenia*: Myrtaceae), it would be difficult for them to be more so. The intermediate values for borokotò - igapo, reflect the presence of species from both flooded and unflooded habitat types. Flood-tolerant species, more commonly found in igapó such as *Licania mollis* (Chrysobalenaceae) and *Microphollis venulosa* (Sapotaceae), occupy the hummocks' lower levels, while terra firme species like *Brosimum parinaroides* (Moraceae), *Chrysophyllum sanguinolentum* (Sapotaceae) and *Eschweilera tessmanni* (Lecythidaceae), were confined to the tops of these mounds, areas which are reported to be inundated only in the very highest flood seasons and even then only for transient periods.

3.6.2 Representativeness of Samples

Standard species accumulation curves are expected to show an extended S-shape, as progressively fewer species are added with further samples until the end point is occurs and the graph reaches a plateau as no further species are added with additional samples. In all cases, graphing data from the quadrat sub-plots indicate that such a plateau is being reached, though full sampling has clearly not been obtained. Use of the linear dependence model of Moreno & Halffter (2000: Section 3.3) indicates that the mean estimated sample completeness was 86% (range 71-96.3: Table III-8). This is, perhaps, not unexpected for igapó where the predominance of hydrochory and ichthyochory among the constituent tree species (Kubitzki & Ziburski, 1994; Mannheimer *et al.,* 2003) means that these will

be widely and generally distributed. Indeed, many of the Rio Negro's frugivorous fish are strongly migratory (Goulding, 1990; Winemiller & Jepson, 2005), with some frugivorous species covering hundreds of km a year. Since seed retention times by Amazonian fish are often measured in days (Anderson *et al*., 2009), or weeks (Gottsberger, 1978), the potential for dispersal by such animals is clearly very great (Goulding *et al*., 1996).

Water dispersal may also carry seeds great distances: Williamson *et al.* (1999) found thet fruits of the hydrochorous legume *Swartzia acuminata* could float and remain viable for up to 81 days. Even given the slow currents of the Rio Negro and Amazon (Goulding *et al.*, 2003), water-dispersal, under such circumstances, clearly provides the potential for extensive dispersal (Kudoch & Whigham, 2001). The majority of igapó species are both abundant and widespread (Merritt & Wohl, 2002), with that many igapó tree species having a much more geographically extensive distribution than their terra firme sister species (Barnett, 1996; Barnett & Lehman, 2000; Gottsberger, 1978). Of Rabinovitz' (1981) seven forms of rarity (*viz* -: 1: locally abundant over large range in restricted habitat type, 2: locally abundant in several habitats, but restricted geographically, 3: locally abundant in specific habitat, but restricted geographically, 4: constantly sparse over large area and in several habitats, 5: constantly sparse over specific habitat, but over large geographical range, 6: constantly sparse and geographically restricted in several habitats, 7: constantly sparse and geographically restricted in a specific habitat), igapó tree species might be expected to lack the four with restricted geographical distribution, leaving only narrow habitat distribution and small local population size (and their combination) as possible rarity forms.

Thus igapó and terra firme will vary in the characteristics of the profiles of their alpha, beta and gamma diversities (*sensu* Whittaker, 1972). Hence, while igapó alpha-diversity (species richness), the beta diversity (in terms of differences between localities) will be small, and alpha diversity and gamma diversity (in terms of the diversity of the whole igapó ecosystem) will likely be very similar if all sub-types are included in the initial sample. This is not the case with terra firme, which is famous for both its alpha-diversity and high beta-diversity based on rapid species turnover over very short distances (e.g. Condit *et al.,* 2002; Duivenvoorden *et al.,* 2002). Thus, at first glance, the level of completeness of the terra firme sample is remarkable indeed given the comparatively small size of the plots, and the comments of Gentry (1988) on the effort needed to obtain even a reasonably near-complete species sample of Amazonian plants species in an area. However, it is common to set the lower sampling limit to 10cm and above. By using 20cm as a minimum, this study may well have excluded a host of small, rare, understory-inhabiting treelets. Thus, though the samples realized the aim of providing a profile of what was most available to a primate species that hardly ever descends into the understory to feed, it is compromised in terms of its comparability with other botanical studies that have used the 10cm DBH minimum.

Tropical forest beta-diversity is often driven by changes in soil type (Clark *et al.*, 1999). Such changes may happen over just a few hundred metres (de Castilho, 2004b). Therefore, it is possible that while the the alpha-diversity of one particular local terra firme community has been well-sampled, it may have occured on just one soil type. Hence it may be giving little idea of neither the extent of beta-diversity, nor of the overall

gamma-diversity of Jaú's mature non-flooded forests. Interpretations of uacari ecology that use these data must, therefore, be regarded with caution.

3.6.3 Phenology

As can be seen from Figs. III-9, 10 and III-11, the great majority of terra firme species (85 of the 107 recorded fruiting, 79%) bear fruit between Oct and Feb, while for igapó the fruiting peak occurs between Jan and Apr. Such patterns are widely reported for these habitats (e.g. Muniz, 2008 for terra firme, and Junk, 1997; Parolin *et al.*, 2002 for igapó). Plants use a variety of developmental an environmental cues to initiate the onset of leaf-flush and flowering (e.g. Reich, 1995). It is likely that differences in community-wide phenological patterns seen between igapó and terra firme at Jaú are due to the use of different sets of environmental cues to initiate flowering and fruiting in the two communities. In Amazonian terra firme the cue for many species is widely believed to be the temperature and insolation changes that accompany the cessation of the rainy season (Alencar *et al.*, 1979; Magalhães & Alencar, 1979; Mori & Prance, 1987a,b; Myneni *et al.*, 2007). This leads to flowering occurring most frequently during the transition from the dry to the rainy season, and fruiting being concentrated in the rainy season (Bentos *et al.*, 2008). By contrast, for the trees of igapó, where hydrochory and ichthyochory dominate (Kubitzki & Ziburski, 1994; de Souza, 2004), the availability of ripe fruit is more tightly peaked (Parolin *et al.*, 2002). The cues for this are thought to be changes in oxygen availability to roots that occur as inundation begins (Maia & Piedade, 2000, 2002a,b). So that mature fruit is ready to be dispersed at the time of high waters, fruiting in igapó begins several months before full inundation. In consequence, igapó has unripe fruit available for many months before dispersal occurs. Similarly, a pulse of anoxic conditions at root level means that leaf drop and flush are highly-synchronized near

community-wide events (Ferreira, 1991), that occur as water levels begin to recede in Aug-Oct (Maia, 1997; Maia *et al.,* 1998). At Jaú, most new leaf records for both individual trees and species occur between Jun and Sep. In terra firm, leaf replacement tends to be less uniform in terra firme, with species replacing leaves in all months (Reich *et al.*, 2004), though it is more common in the dry season and wet/dry transition (Kim *et al.,* 2007). These contrasting patterns of fruit and leaf availability in the adjacent habitats of terra firme and igapó have important consequences for uacari foraging ecology.

3.6.4 Crop Volumes

Crop volume data were calculated for 19 species of tree from igapó and for 9 species of tree from terra firme. The full significance of these data will be considered in Chapter 5 where they contribute to the study of choice ratios of diet items

Flowers: crop sizes and the extent of their intra-annual variation

Eschweilera tenuifolia was (numerically) the main source of flowers in the diet of *C. m. ouakary* (Chapter 5), but trees showed considerable variation in the number of flowers between the two years over which flowering was measured. In 2007/8, the mean number of flowers per m² of canopy was 4.23 (SD±1.69, N=15). In 2008/9, this value was 1.04 (SD±1.04, N=12). With only two years of data, it is impossible to distinguish between a simple bad year following a good one and a regular high-low oscillation. However, each annual pattern was common to almost all *E. tenuifolia* trees, and the alternation was said by local people to be a regular feature of the macacaricuia tree population. If this is a true long-term pattern, it is significant for two reasons: firstly, because uacaris feed directly on *Eschweilera* flowers between Jan and Mar, and when they are abundant these flowers are a numerically important part of the diet (Chapter 5), and secondly because the flowers

that survive to be pollinated provide a fruit that is also a key diet element (Chapter 5). So this variation in flower crop is important because it indicates that the volume of key resources available to the uacaris may fluctuate between years. This is especially significant since this floral proxy provides the only measure available to the current study of such supra-annual variation, since floral crop was measured in both years, but fruit crop was measured in only the second year of the study. However, qualitative data suggest that 2006-7 and 2008-9 were both heavy crop years for *E. tenuifolia*, while 2007-2008 was a year in which there was a light *E. tenuifolia* crop. Similar variation was observed qualitatively for *Mabea nitidans* and *Amanoa oblongifolia*, which had light crops in 2006-7 and 2008-9 and abundant ones in 2007-8.

Codonanthe crassifolia was the only plant from which flowers were eaten in all phases. *Codonanthe* vines have been also recorded as flowering throughout the year elsewhere in Amazonia (van Dulmen, 2001). Over the observation period, 20 of the 23 vines had flowers. Sampled flowering plants varied in area from 33 to 212cm² (mean 95 08cm², SD±49.58), and bore from 2 to 33 flowers (mean 10.91, SD±9.26). *Codonanthe* vines were present on 66 of the 100 igapó trees sampled for them. Epiphyte communities on Neotropical trees can be enormously complex and abundant (e.g. Freiberg, 1999). But in igapó they seemed sparse, and *Codonanthe* appeared to be the only one regularly in flower in all months.

3.7 Conclusions: Consequences for Uacaris of Botanical Composition Patterns

The data have shown that the igapó flora has plants whose fruits have synchronous peaks of fruiting and of leaf-flush that are off-set from each other and, to a lesser extent, from that of terra firme. With the exception of the species-rich high-evenness sub-community

at the igapó margin, the overall species diversity patterns of the igapó plant community are, when compared with neighboring terra firme, more like that of a temperate forest, with large numbers of individuals of a few species of tree. In contrast, in the neighbouring terra firme, the majority of species are represented by one or two individuals. In addition, evenness in igapó is further reduced on a sub-community level: comparing the data from the three non-margin quadrats shows that two or three species tend to dominate one area of the igapó, and a different set will then be numerically more abundant in another area which endures greater or lesser inundation length. This is likely related to differences in inundation duration and species' tolerance. This results in a horizontal banding within the igapó community, and the presence of these sub-communities may have strong consequences for the composition of uacari daily diets (Section 5.3), and their movement patterns.

Though not quantified, field observations suggest that within these inundation-tolerance defined sub-communities clumping of individual tree species is relatively rare. It occurs for palms such as *Leopoldinia* (Kubitzki, 1991) and fire-dependent species such as *Duroia,* but otherwise appears to be mitigated against by the randomizing effects of water and fish-based dispersal, which produce extensive but diffuse seed shadows for individual trees (Kubitzki & Ziburski, 1994). This also has consequences for the uacari diet. The offsetting of fruiting periods probably act as a driver for between-habitat migration. The period of fruit dearth is, however, near-synchronous in flooded and non-flooded habitats. This period coincides with leaf-flushing and (not recorded in a quantified way, but observed in the field) the production of new shoots. This forces seasonal diet change in the golden-backed uacari at Jaú (chapters 5 and 6).

CHAPTER 4:

BEHAVIOURAL OBSERVATIONS

I wish I knew half what the flock of them know
Of where all the berries and other things grow,

T.S. Eliot, *Sweeney Agonistes*

4.1 Introduction

The chapter includes sections on the how golden-backed uacaris interact with each other (Section 4.3.7), with the physical environment (Section 4.4.4), and with other species (Section 4.4.7), both as perceived predators and as collateral providers of foraging opportunities. Detailed data on diet and feeding are presented in Chapters 5 and 6.

4.1.1 Aims

This chapter presents the results of field observations on the behaviour of *C. m. ouakary* at Jaú National Park, Brazil. The general behaviour of the golden-backed uacari has not previously been the subject of detailed studies, with the only published material being the result of short-term investigations (da Cunha & Barnett, 1990; Barnett & da Cunha, 1991; Barnett *et al.*, 2002, 2005; Defler, 2004). Accordingly, to provide a basis for comparison with other uacari taxa (*C. c. calvus*: Ayres, 1986a,b; *C. c. ucayalii*: Bowler, 2007; *C. m. melanocephalus*: Boubli, 1997a), the following aims were pursued, to:

- describe behaviours and vocalizations
- provide time budget
- record how uacaris use forest strata
- delineate features of sleeping trees
- gain an understanding of uacari social organization
- record basic reproductive parameters.

To provide data on additional factors which might influence foraging, I also recorded reactions to potential predators (raptors, carnivorous mammals), and to other vertebrates which the uacaris encountered.

At Jaú, there are three distinct annual phases of resource availability in the igapó-terra firme forest association. These have been described in Chapter 3. They provide a framework against which the relationships between ecology and behaviour could be tested. Accordingly, a series of secondary aims was elaborated, designed to test the null hypotheses that:

- time budget does not vary between phases
- habitat choice does not vary between phases
- uacaris breed randomly across the year, with no association with patterns in resource availability.

Data on diet use by phase are presented in Chapter 5. Aspects of foraging are presented in Chapter 6.

4.2 Methods

4.2.1 General Methodology

The field visits made between Oct 2006 and Mar 2007 served to habituate the uacaris to the presence of observers, to allow the recognition of the salient components of the uacari behavioural repertoire, and provide opportunities to become familiar with the best ways of recording them. Data from these months are excluded from the quantitative analysis, which therefore includes only data from Apr 2007-Apr 2008. However, *ad lib* data from the habituation period are included where appropriate.

4.2.2 Daily Routine

Studies in igapó were made from small wooden canoes (Fig. II-13). It was unsafe to work in these in strong rain or high wind, which might have resulted in swamping, or being hit or sunk by falling branches. Fieldwork therefore began as close to 06.00 as weather permitted, and was terminated if strong rain or winds persisted for more than 30 mins. Igapó fieldwork was confined to three areas (Fig. II-5). One of which (Area A, 'Parana') was on the eastern bank of the Rio Jaú, another (Area B, 'Furo da Moa') was on the western bank, and the third (Area C, 'Ilha de Macaco') was a 74ha island of igapó, which has been isolated for some 15 years (Eduardo de Souza, pers. comm.), and lay in-between the other two. Unless animals had been contacted in a study area the evening before, all areas were checked until a band was found. Starting order was randomized to prevent over-sampling. In any one area, a guide and I paddled and searched for recent feeding debris, or auditory or visual contacts. If no contact was made within 30 mins., the next nearest area was investigated. This rotation continued until animals were contacted. Animals were then followed until lost. When it became apparent that no further contact was possible, we returned to base to allow botanical specimens to be processed, photographed and curated. In the afternoons we adopted the same procedure and tried to follow the animals until they settled in sleeping trees, though this was rarely achieved (N=43 trees, 15 evenings). When a band was contacted, either the largest or the closest sub-group was chosen and followed. If that was lost, we followed the next one that we found and could keep up with.

In terra firme, animals were observed if they were encountered when I, or a field assistant, were on one of the survey trails or visiting the non-igapó phenological plots. A system of interconnecting trails, such as was implemented by Boubli (1997a) for the

study of *C. m. melanocephalus* in non-flooded forest, was not put in place, so it was necessary to move through uncut undergrowth. This often resulted in the cessation of uacari activity and initiation of flight. Consequently, most observations of uacaris in terra firme were made from available high ground or the crotch of a small tree, animals being observed until they were out of sight. On days designated as primate observation days but on which no uacaris were found, field time was used to, for example, sample non-sleeping trees for lianas, conduct supplementary observations on comparative feeding behaviour of birds that associated with uacaris, measure crop volumes and other comparative measures that provided data against which the characteristics of forest features used by uacaris could be statistically compared.

4.2.3 Identifiability of Individuals and of Bands

It was not possible to identify individual animals reliably, due to the lack of features that have been used in other primate studies such as facial markings or variation in vocalizations (Butynski *et al*., 1992; Price *et al.,* 2009) or body colour patterns (Bradley & Mundy, 2008; Schiel *et al.,* 2002; Ron & Whitehead, 1993). For this reason, with the exception of the single band of uacaris on Ilha de Macaco, it is not possible to assert unambiguously that the same bands were studied on every encounter with uacaris at the Parana and Furo de Moa sites.

4.2.4 Visibility

Visibility differed greatly between igapó and terra firme. For 10 of the 13 months that comprised the Main Study, observations were made in flooded igapó with most understory vegetation underwater. In contrast, the understory was always thick and shoulder high in terra firme (compare images in Fig. II-4). Thus, though both tree density

and mean basal area per m² were higher in igapó than terra firme (0.72 per m² and 62.6cm, respectively for igapó *vs.* 0.49 per m² and 53.7cm for terra firme), there were substantial differences in effective understory plant density between the two. Lianas densities also varied, constituting, for example, 4 of 361 (1.1%) enumerated plants in igapó quadrat 3, but 14 (5.8%) of 241 plants of the terra firme study plot. This is of practical importance since lianas impede views of the canopy, the zone in which uacaris are active. In addition, igapó canopy is generally lower than terra firme's (Parolin *et al.*, 2002). This, combined with the presence of several metres of floodwater, meant that observer-to-canopy distance was much less in igapó than terra firme. Consequently, in igapó it was often possible to see uacaris clearly at distances ≥ 250m, while in terra firme the greater density of vegetation meant that visual contact at distances ≥ 100m was possible only intermittently.

4.2.5 Scans

Sampling methods

Behavioural sampling began in Dec 2006. From then until Apr 2008, I obtained 1,563 observation blocks, comprising 4,484 instantaneous scans. Across the period from Apr 2007-Apr 2008, when data were being gathered quantitatively from habituated animals, the mean all-habitat monthly contact time was 558 mins. (range, 192-801 mins.). Table IV-1 shows the distribution of contact time and of scan samples per month per habitat, including the data from additional months surveyed by Ms. Almeida.

Table IV-1: Behavioural Sampling of* Cacajao melanocephalus ouakary *at Jaú National Park During Pre- and Post-habituation Period

(number in bold italics are pre-habituation; numbers in grey are post-habituation)

	Totals				***Terra Firme Contact Time***				***Igapó Contact Time***			
Month	***No. Search Days***	***No. Contacts***	***Total No. Scans***	***Total Mins*** [1]	***No. Search Days***	***No. Contacts***	***No. Scans***	***Total Mins***	***No. Search Days***	***No. Contacts***	***No. Scans***	***Total Mins***
Oct 06	***6***	***6***	***0***	***256***	***2***	***0***	***0***	***0***	***4***	***6***	***0***	***256***
Nov 06	***8***	***0***	***0***	***0***	***3***	***0***	***0***	***0***	***3***	***0***	***0***	***0***
Dec 06	***6***	***5***	***80***	***192***	***3***	***1***	***30***	***153***	***3***	***4***	***50***	***39***
Jan 07	***9***	***17***	***100***	***178***	***3***	***6***	***50***	***99***	***6***	***11***	***50***	***79***
Feb 07	***12***	***20***	***378***	***433***	***2***	***3***	***101***	***79***	***10***	***17***	***277***	***354***
Mar 07	***11***	***22***	***215***	***365***	***2***	***0***	***0***	***0***	***9***	***22***	***215***	***365***
Apr 07	9	14	238	378	2	0	0	0	7	14	238	378
May 07	12	17	326	577	2	0	0	0	10	17	326	577
Jun 07	8	9	198	355	2	0	0	0	6	9	198	355
Jul 07	0	--	--	--	--	--	--	--	--	--	--	--
Aug 07	12	11	740	811	2	0	0	0	10	11	740	811
Sep 07	17	15	488	621	2	0	0		8	15	488	621
Oct. 07	0	--	--	--	--	--	--	--	--	--	--	--
Nov 07	0	--	--	--	--	--	--	--	--	--	--	--
Dec 07	16	[5]13	127	232	6	[2]3	0	66	10	[3]10	127	166
Jan 08	12	[3] 15	527	456	4	[0]2	0	228	8	[3]13	527	228
Feb 08	0	--	--		--	--	--	--	--	--	--	--
Mar 08	19	[1] 15	579	855	6	[0]0	0	0	13	[1] 15	579	855
Apr 08	14	[0]15	488	748	4	[0]0	0	0	10	15	488	748
Total	**171**	**[203] 194**	**4484**	**6457**	**46**	**[16] 14**	**181**	**625**	**115**	**[186] 179**	**4395**	**5832**

Note: [1] from Sep 2007 until Apr 2008, additional records of uacaris made by Thais Almeida are recorded in square brackets. Ms. Almeida continued to work from May 2008 until Sep 2008, but did not contact uacaris in either habitat during this period.

Of the 1,563 blocks, 681 were composed of sequences of 90 seconds duration or less (three sequential scans or fewer). These were excluded from the analysis since they operated as a potential bias in favour of short-period or very obvious behaviours. A further 78 blocks were excluded as they sampled adolescents who were recorded as spending > 50% of their recorded time playing and were never observed feeding, though they clearly must have done so, Another 14 blocks were excluded because sheets were spoilt. Time budget analysis therefore uses only the 794 blocks that were part of sequences of 120 seconds or longer and which came from adult animals. To calculate the time budgets, the percentage of each of the five behaviour categories was summed for each block, and these were then averaged to give the time budgets presented in figs. IV-2

and IV-3 and in Section 4.3.2. This was done because the blocks varied in duration from 120 to 300 seconds, and it was necessary to avoid bias from the longer samples.

Data in this chapter which do not come exclusively from scans include data used for the ethogram (Appendix IV-2), nearest neighbour distances (Section 4.3.4), forest structure use (Section 4.3.5), sleeping trees (Section 4.3.6), and vocalizations (Section 4.3.7). Details of how additional data were collected are included in the relevant section. With the exception of time-budget considerations, data relating to diet are not presented here, but appear in chapters 5 and 6.

Definitions

Only data from adults are used in calculating time budgets. However, non-adults are used at other points. Non-adults were simply categorized as 'adolescents', 'juveniles' or 'infants', since there have been insufficient studies to permit their categorization to developmental stage, as has been done with better-known Neotropical primates (e.g. Baldwin & Baldwin, 1973, 1978; Neville, 1972 with *Alouatta*). Allocation to developmental class was size dependent, and followed Fontaine (1981) for *C. c. ucayalii, viz*:

Infants -: approx. one-quarter the body length of the mother

Juveniles -: approx. one-half the body length of the mother

Adolescents -: approx. two-thirds the body length of the mother[1]

([1] the use of the term 'mother' is an assumption based on the persistence of proximity, it does not imply a confirmed genetic relationship. Animals that had yet to achieve adult size were always compared when within 5m of an adult, permitting a reliable comparison of size to be made).

For calculation of a time budget, observed behaviours were recategorized from those classifications given in Table II-8 (Section 2.12), and grouped into one of five broader categories, given in Table IV-2.

Table IV-2: Definitions of Behavioural Categories Included in Time Budget

Behaviour Category	***Definition of Behaviour***
Feeding – paused	Locomotion slow and restricted to a feeding path of one or more adjacent tree crowns, or one or more concentrations of germinating seedlings. Plucking, processing and ingesting the principal activities. Combines 'Feeding-procuring' and 'Feeding-Processing' categories of Table II-8, if not occuring during movement between tree canopies.
Moving – feed	Food plucked in transit and either eaten in transit or during brief stops of less than 30 seconds. Principal activity is locomotion, but with food item(s) held in hand and/or mouth. Combines 'Feeding-procuring', 'Feeding-Processing' with 'Moving-foraging' categories of Table II-8, during movement between tree canopies.
Moving – travel	Locomotion, un interrupted by obtaining or processing food, or moving with food held in a hand or mouth but with no pause for feeding.
Resting	Cessation of locomotor and of food-related activities. Either sitting or lying on branch. Includes self grooming.
Social	Grooming – cleaning movements of body with teeth, mouth and fingers – either of own body or that of another individual. Plus other social behaviours, inc. play, fighting, mating.

4.2.6 Definition of Band, Group and Sub-group

Kummer (1971) appears to have been the first to introduce the term ''fission-fusion'' into primatology, when he used it to describe the tempo-spatially fluid social systems of *Papio gelada, P. hamadryas* and *Pan troglodytes.* As noted by Aureli *et al.* (2008) and by Kappeler & Van Schaik (2002), there is no dichotomy between highly cohesive and very fluid social organizations in primates, but rather the systems like *Propithecus* and *Pithecia* (cohesive), and *Ateles* and *Chiropotes* (fluid) represent a continuum of potential fission-fusion dynamics. Practically, this flexibility has posed problems in defining such study entities as 'group', 'sub-group' and other sub-divisions. These problems have included both the function of such entities and how to define them operationally in the field (Emery-Thompson & Wrangham, 2006). Symington (1990), working on *Ateles* and *Pan*, offered an operational definition of a sub-group as a number of animals which,

although behaving and moving coherently, are consistently separated by at least 25m from a conspecific association displaying equal properties of spacing and movement. This rule-of-thumb has since been applied to a number of other primate species with fission-fusion spacing behaviour (e.g. *Varecia rubra*: Vasey, 2006; Natalie Vasey, pers. comm.). Given the potential difficulties in separating sub-groups in a species that moves quickly, where individuals are often very widely separated (Table IV-5) and where sub-groups are often very diffuse (Table IV-6), this canonical definition served as a convenient minimum spacing. In fact, mean inter-subgroup distance was substantially greater than 25m (sections 4.3.4 and 4.4.3). Whenever there was ambiguity as to whether two sub-groups were in fact one larger sub-group it was assumed to be one big band and the numbers combined for the total count.

A group was defined as a number of sub-groups that were moving in the same direction in the same area of forest at the same time, which appeared to be in auditory contact, but which had a uacari-free gap of less least one modal group spread (200m) between them and at least a 200m gap between them and other group (if any other should be in proximity).

In such contexts, use of the word 'group' causes problems since it is both a common collective noun, and perceived to be of a higher-order grouping in uacaris and other fission-fusion species (Aurelli *et al*., 2008). Here, I follow Heymann (1992a)'s three-tier naming system for spatially contiguous occurrences of uacaris of varying numerical strenghs: '*unit'* > 10 individuals, '*group'* for 25-50, '*troop'* for 51 - 100+ individuals. However, when talking in broad terms I use the term 'band' as a general collective noun for any number of golden-backed uacaris associating in the same time and place.

4.2.7 Group Spread and Inter-individual Spacing

Group spread was recorded at first contact each day and also subsequent contacts in the day that followed from when a group had been lost and after any significant event (such as group fission or fusion). Distance between individuals was recorded as a standard part of the scan process (Section 2.12).

4.2.8 Sleeping Trees

A sampling regimen was designed to elucidate not only what species were chosen as sleeping trees, but if the trees were being chosen randomly, and, if not, what, if any, special properties they possessed that might explain the choices of these trees and not others. In addition to characterizing the tree species, DBH, canopy height and extent, I also recorded the distance to nearest dry land, distance to nearest water without emergent woody plants, and the distance to next sleeping tree in use the same day by the same band. Data were compiled for 43 sleeping trees used by the uacaris between Feb 2007 and Jan 2008. It was also noted if the tree had been previously recorded in use as a sleeping or feeding tree, if one or more animals were observed sleeping there, and where in the canopy sleeping occurred. The presence/absence of lianas and of ant and wasp nests was also noted on all sleeping trees and their cumulative frequencies compared against those counted on 100 randomly selected trees (Section 2.14).

4.2.9 Use of the Forest

This covers the uacaris use of particular forest strata, as well as branch sizes, liana types, and parts of the canopy used. Estimation of absolute height above ground was complicated by the dramatic annual flux of floodwaters (> 10m in some parts of the study igapó). Height data are therefore not reported here. To determine if preferences existed for lianas, branches and canopy part (i.e. trunk and near-trunk, mid-canopy,

canopy edge), as part of each scan I recorded the size of the branch and the part of the canopy the animals occupied at the moment of observation (whether on- or off-scan).

4.2.10 Testing for Habituation

A habituation period has long been a part of the standard methodology of field primatology (Setchell & Curtis, 1999). This is because has long been recognized that not only are non-habituated animals harder to find and to observe, but since the response is to a perceived predator, non-habituated (i.e. threatened-feeling) animals may bunch closer together, spend less time resting, spend more time foraging on the move, move less conspicuously in denser vegetation and forage on items that are quicker to obtain and more rapid to process (Miller, 2002; Williamson & Feistner, 2003).

For a study such as the current one, where the effects on the animal's diet and behaviour of strong seasonal variation in resource availability are being investigated, it is clearly essential to remove the effects of reaction-to-observer from the list of variables. Sub-group sizes may also be a response to changes in resource availability (e.g. Asensio *et al.*, 2008; Vasey, 2006), and at Jaú there are substantial levels of variation in resource availability across the months surveyed. However, Chapman *et al*. (1993) note that apparent changes in group size may indicate progressively greater levels of habituation. Chapman *et al*. (1993) also observed that progressive diminution of distance to a study group is a good practical measure of increasing habituation. Accordingly, to test if habituation was occurring, I compared the mean of distances between observed animals and myself for each month that observations were made. I only used as data those blocks of scans that lasted 90 seconds or more. Results are presented in Section 4.3.1.

4.2.11 Methods for Studying Associated Species

Preliminary field studies in Jaú in 1999, 2000 and 2005 had shown that uacaris rarely associated with other primates, and were rarely followed by insectivorous birds. However, predation on a uacari by a harpy eagle (*Harpia harpyja*: Accipitridae) had been witnessed in 2005 (Barnett *et al*., in press), and scattered qualitative observations existed of uacaris responding nervously to overflying birds, even species that were non-raptorial (e.g. toucans: Boubli, 1997a). Jaú has a low human density, little hunting occurs and an apparently high density of mammals and birds (Borges *et al*., 2004b). I therefore wished to know if the presence of raptors impacted on uacari feeding behaviour. Investigating these aspects was secondary to the uacari-based field aims and so data-collections were somewhat *ad hoc*, occurring whenever and wherever there was a gap in uacari-based data collection. The following protocols were employed:

Raptor surveys

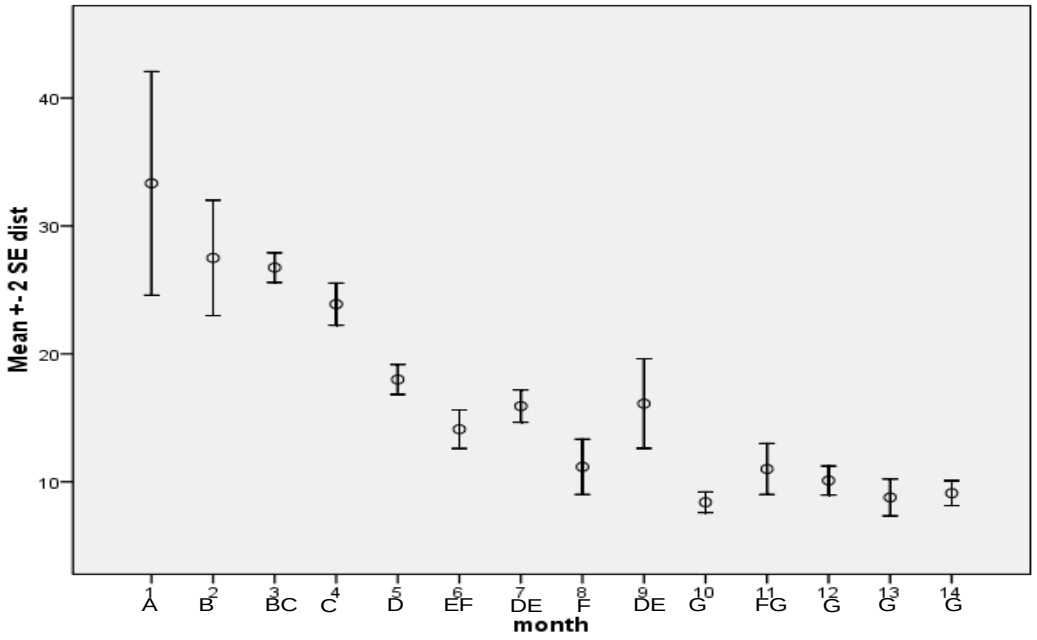
Between Jan and May 2007, I conducted monthly raptor surveys using a transect from the mouth of the Jaú River to the research base, a distance of some 45 linear kms (probably around 70km when river bends are included). Counts were conducted in fine weather only and occurred between 08.00 and 14.00 (heading upriver) and 16.00 to 18.00 (heading downriver), and were made from a moving small boat. I also surveyed for raptors from moving canoes during return from fieldwork (raptors rarely being active in the early morning hours). In both cases I concentrated on flying or soaring birds. Species were identified and the number of contacts recorded per observation hour (or part thereof). I did not attempt to correct for repeat recording of the same bird as it moved relative to my position on the winding river course.

Predator-response observations
When following or observing uacaris, my guide and I listened for calls and looked for birds flying over the uacari band or flying near to them. Species were identified and the reactions of the uacaris were then recorded *ad libitum.* Likewise, reactions of uacaris to non-volant vertebrates (such as iguanas, anteaters, sloths) were recorded, as were their reactions to any mammal calls (e.g. jaguar).

Associations with, and reactions to, other primates
Whenever non-uacari primate species were encountered, the size and composition of the band, its habitat, stratum, and activity were recorded. Diet items were collected if feeding was occurring. If the band was in visual or auditory range of uacaris (at least as perceived by me), then the reaction of the uacaris to the presence of the other primates was also recorded in an *ad hoc, ad libitum* format.

4.3 Results

4.3.1 Testing for Habituation
Fig. IV-1 presents monthly means, with 2 SEs, for observer-subject distance for observations which lasted more than 90 seconds for 14 months between Oct 2006 and Apr 2008. Oct 2006 to Mar 2007 had been designated as the habituation period. The data were compared using Duncan's 1-way ANOVA as a post-hoc test to examine whether monthly means declined over time. Difference blocks ($P < .05$) are labeled A-G on the x-axis.



Key to months: 1=Oct06, 2=Dec06, 3=Jan07, 4=Feb07, 5=Mar07, 6=Apr07, 7=May07, 8=Jun07, 9=Aug07, 10=Sep07, 11=Dec07, 12=Jan08, 13=Mar08, 14=Apr08.

Fig. IV-1: Mean Animal-observer Distance (m) per Month in Igapó Forest (2006-2008)

If animals gradually came to accept the observer during the Initial Period and continued to do so once habituation was achieved, then it would be predicted that mean observer-animal distances would gradually decline over time during the Initial Period and remain constant thereafter. To test for differences between months I used Spearmen's Rho to measure the rank correlation coefficient between the two variables (where Oct = observed month 1, Dec = observed month 2 etc.) for the first 12 months of the post-habituation period. The result of this is a significant negative correlation ($R_s = -.932$, $p < .001$, $N=14$), indicating that observer-uacari distance decreased over time. This is taken to indicate that the level of habituation increased with time. However, the decline was not gradual and there was a period of rapid decline occurred between Mar and Apr 2007 (Fig.

IV-1). Distances continued to decline throughout the study, though there is an indication of a plateau being reached in the last three months (ending Apr 2008, Fig. IV-1). This suggests that the habituation was effective, and that animals were sufficiently habituated from Apr 2007 (the start of the Main Period of field work) for fieldwork data to be considered sufficiently free of flight-based variables to be a reliable indication of day-to-day uacari behaviour.

However, caution is advisable. Because the decline continued almost throughout the entire period of observation, it cannot be confidently asserted that the animals were fully habituated for the entirety of the field study's Main Period.

It should be noted that the probable failure by the current study to fully habituate a study group for, at least, the great majority of the field period is not unique in uacari-based field work. Ayres (1986a) refers to his *C. c. calvus* study animals as 'incompletely habituated' and though Boubli does not make an explicit statement about the levels of habituation of his study animals, the long periods between his contacts with *C. m. melanocephalus* groups make it unlikely that full habituation was achieved during his 120 hrs. of contact, spread over 16 months of field study.

4.3.2 Time Budgets

Table IV-3 displays the montly percentage of scans allocated to five pre-defined behavioural categories (794 observation blocks for adult uacaris). All data come from the post-habituation period. Table IV-4 represents these data for the three phases of resource availability discussed in Chapter 3, but summarize here for convenience: Phase 1: (Nov–Feb), the igapó poor in both fruit and new leaves, but fruit is present in terra firme; Phase 2 (Mar-Jun) the igapó has abundant fruit, is poor in new leaves; Phase 3 (Jul-Oct) the

igapó is rich in new leaves, but is poor in fruit. Fig. IV-2 gives the Annual Time Budget as a graphic and Fig. IV-3 does the same for the three phases of resource availability.

Table IV-3: Monthly Time Budget for Golden-backed Uacaris at Jaú

Month/Behav.	*Paused Feeding*	*Moving Feeding*	*Moving Travel*	*Rest*	*Social*
Apr 07	37.9	6.1	42.9	8.9	4.2
May 07	38.8	6.2	44.7	6.4	4.1
Jun 07	36.7	8.6	42.2	7.0	5.5
Jul 07	--	--	--	--	--
Aug 07	29.7	18.4	49.9	0	0
Sep 07	27.8	15.2	43.7	8.8	4.5
Oct 07	--	--	--	--	--
Nov 07	--	--	--	--	--
Dec 07	24.1	9.4	59.6	0	6.9
Jan 08	29.4	7.4	59.2	0	5.0
Feb 08	--	--	--	--	--
Mar 08	31.8	8.5	45.9	8.4	5.4
Apr 08	39.9	9.5	44.8	5.8	0
Mean Total	***32.9***	***9.9***	***48.1***	***5.1***	***4.0***

Note: '—' indicates months when no data was collected, '0' indicates data in this category was not recorded during scans.

Table IV-4: Mean Time Budgets of adult* C. m. ouakary *across Three Phases of Resource Availability at Jaú

Month/Behav.	*Paused Feeding*	*Moving Feeding*	*Moving Travel*	*Rest*	*Social*
Phase 1 (in terra firme)	26.6	8.4	59.3	0	5.8
Phase 2 (abundant fruit)	37.0	7.7	44.1	7.3	3.9
Phase 3 (fruit dearth)	28.7	17.8	46.8	4.4	2.3

Based on observations in the following months: Phase 1 (terra firme use, Dec-Jan), Phase 2 (months of fruit abundance in igapó, Mar-Jun), Phase 3 (fruit dearth in igapó, Aug-Sept)

Though there is some variation in the values for the categories between phases, the proportions remain roughly the same throughout. The most notable change is the increase in the amount of paused feeding in Phase 2 and of moving feeding in Phase 3. How these changes relate to patterns of resource availability in these phases is discussed in Chapter 6.

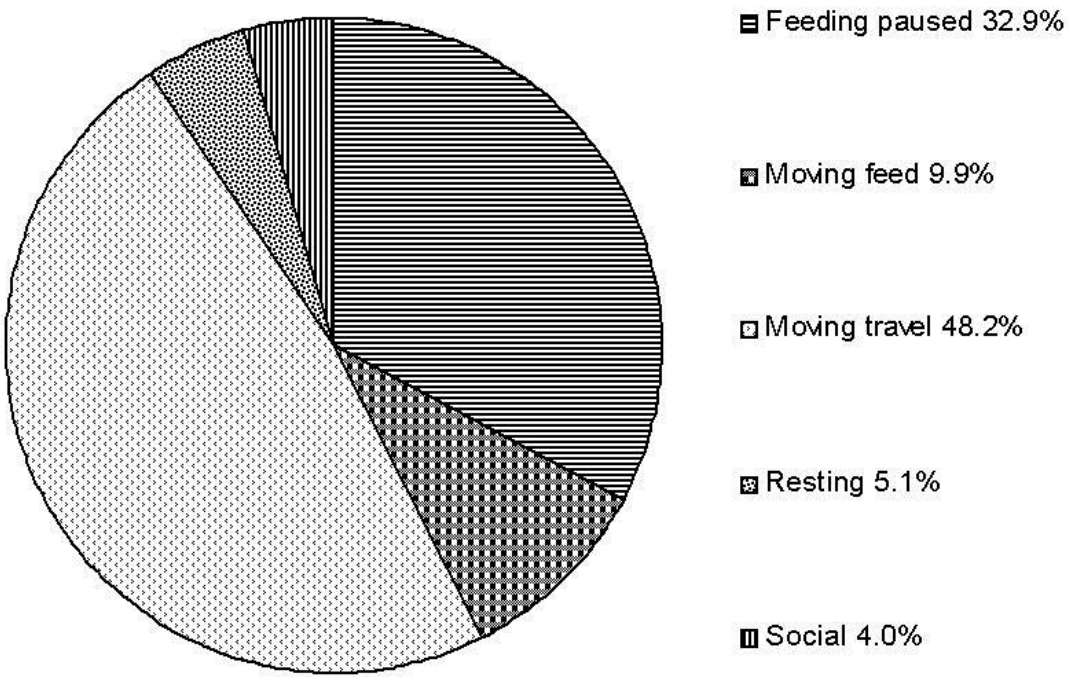


Fig. IV-2: Annual Time Budget of Adult* C. m. ouakary *at Jaú National Park, Brazil.

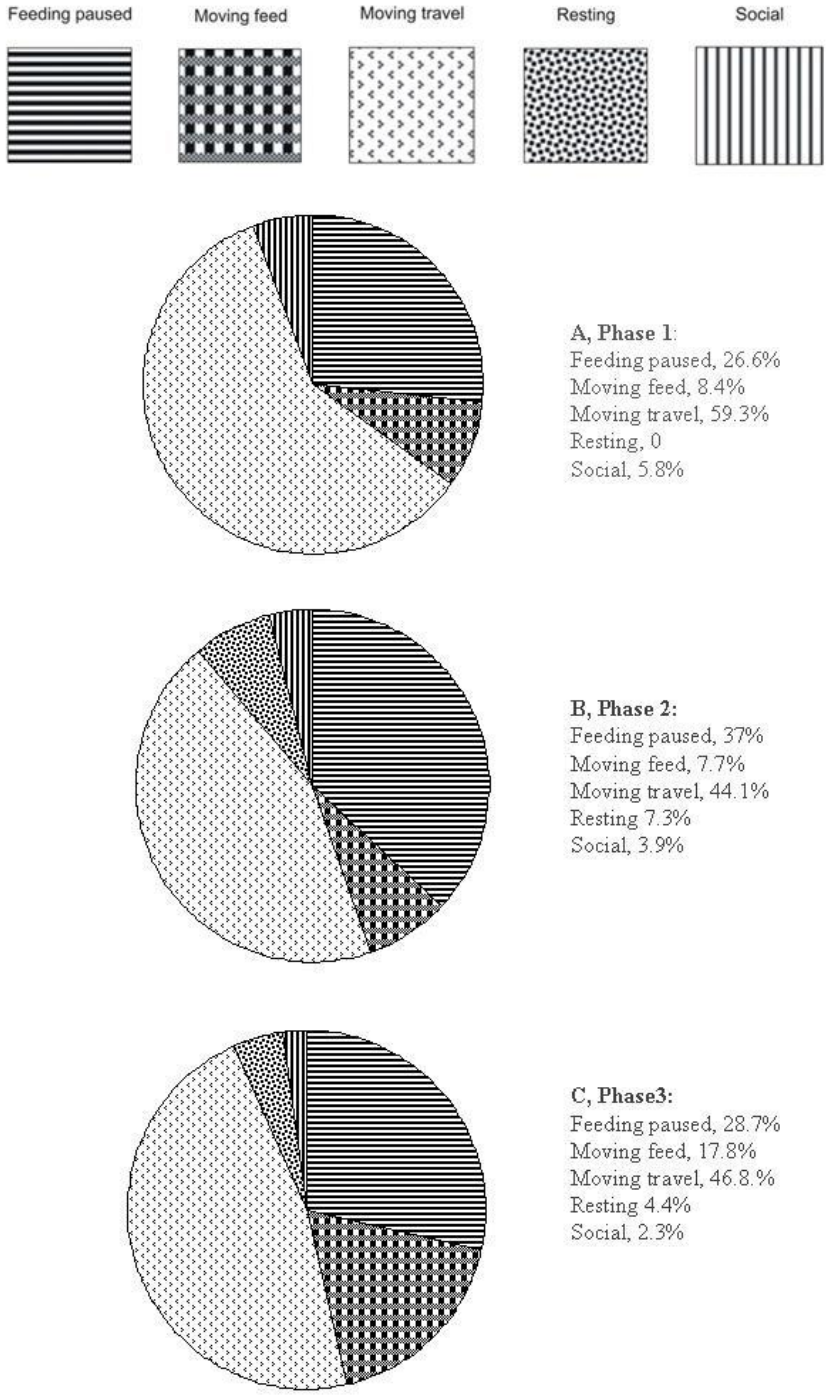


Fig. IV-3: Proportions of Five Behavioural Categories in the Three Different Phases of Resource Availability.

A, Uacaris in terra firme; B, Uacaris in igapó, abundant fruit, few young leaves; C, Uacaris in igapó, few fruit, abundant young leaves

4.3.3 Reproduction

Females with very young infants, all approximately equal size, were seen in Dec 2006 (N=1), Dec 2007 (N= 4), and May 2007 (N=11), but in no other months.

4.3.4 Size and Structure of Social and Foraging Bands

General patterns of spacing

Nearest neighbour mean distances (NND) and group spread were calculated using data from the 794 blocks of scans used to calculate time budget (less 20 instances for which NND measures are missing, N=774). To this I added the 78 blocks of scans for adolescents and 18 NND records of sexed males made during *ad libitum* observations (N=870). A block could contain data on 1, 2 or 3 animals (method trials made during the habituation period showed that I could not guarantee keeping track of more than three animals). Because of this, results were calculated directly from the 3490 scans that made up the 870 blocks, with each scan being treated as an independent sample. There were 1266 NND records within bands. A further 79 records were of isolated animals travelling alone, and a further 4 of a solitary dam with a dependent clinging infant. Mean values from all months combined are given in Table IV-5. Table IV-6 gives summed annual values for group spread as a function of band size. The relation of these data to group behaviour is discussed in Section 4.4.3. Data on NND and band size per Phase will be discussed in Chapter 6.

Table IV-5: Mean Nearest Neighbour Distances (m) for Identifiable Males, Females-with-infants, Unsexed Adults and Adolescents (all months and habitat combined)

Age Class	*Mean NND*				*N (%) of Additional Records from Single Individuals*[1]
	N	*Mean*	*SD*	*Range*	
Sexed male	30	5.5	2.43	5 - 22	9 (23.1)
Female with baby	298	2.2	2.42	1 - 19	4 (1.3) (=mother-baby diad alone)
Unsexed adult	550	4.3	8.5	1 - 22	68 (11)
Adolescent	388	2.8	2.23	1 - 16	2 (0.5)
TOTALS	**1266**	**3.7**	**3.89**	**1 - 22**	**83 (6.2)**

[1] *counted as 'single' if no other uacari was audible or visible. If other animals were audible and only one animal was seen, this animal was considered to be part of widely-dispersed group.*

Table IV-6: Frequency of Spread of Uacari Groups in Igapó

Group spread	*No. Animals*					
	2-5	*6-15*	*16-25*	*26-40*	*41+*	*Totals*
To 20m	*9*	*0*	*0*	*0*	*0*	***9***
21-50m	*18*	*2*	*0*	*0*	*0*	***20***
51-100m	*0*	*2*	*6*	*0*	*0*	***8***
101-200m	*19*	*34*	*6*	*4*	*0*	***63***
201-275m	*9*	*18*	*12*	*9*	*1*	***49***
Totals	***55***	***56***	***24***	***13***	***1***	***149***

Note 1: *There were also 79 records of single animals (Table IV-5), and a further 4 of females travelling alone while carrying a dependant infant. Group spread was not recorded for an additional 40 encountered groups.*

Note 2: While it was often possible to see to 250m (Section 4.2.4), *275m represented the absolute maximum at which distance could be recorded reliably at the speed required for fieldwork without undue interference by intervening vegetation.*

Groups of ≥ 41 animals were encountered in igapó (Table IV-6). The most frequent size was between 6 and 15. Bezerra *et al.* (in press) have reported band sizes of between 2 and 26 individuals. I also obtained measures of the distance between foraging or moving bands of uacaris, using the 25m separation rule of Symington (1990) to delineate separate sub-groups within a band (Section 4.2.6, for definitions). The mean of 99 measures made from 56 separate daily contacts was 116.6m between such sub-groups.

4.3.5 Use of Forest

Lianas, branches and part of canopy

As part of each of the scan process, size of branch being used and the part of the canopy the animals were in at the time of observation were recorded (Section 2.12). Data refers to the period following the initial habituation period, and includes scans from non-adult animals (Table IV-1). The number of scans used (3791) therefore exceeds the number (3246) used for calculating time budgets. In 149 scans across all three phases (3.9% of 3791 scans), uacaris were recorded in non-tree substrates (low vegetation or on the ground: Table IV-7). In another 277 (7.3%) scans, uacaris were observed using lianas,

and in 17 scans (0.45%) uacaris were on a tree's main trunk. In all other scans uacaris (88.35%) were observed in branches of trees (below).

Use of canopy layers

Table IV-7 gives the percentages of all annually summed observations of uacaris for moving, feeding or resting from the three canopy levels (shrubs, understory trees, canopy and emergents). Because the substrate could change during the course of a series of scans in a block, the data from the individual scans themselves were used rather than the averaged-data-per-block used for calculating time budgets. Data are therefore derived from all scans that were part of block sequences greater than 120 seconds duration, less 65 scans where the behaviour was categorized as ''other'' (N=3, 246).

Table IV-7: Uacari Forest Strata Usage by Behaviour (all Phases combined)

Behaviour	***Forest Stratum (%, N records)***					
	Emergent	***Canopy***	***Sub-canopy***	***Shrub***	***Ground***	***Total %s***
feeding-paused (N= 1068)	7.7 (250)	20.0 (648)	4.00 (130)	0.55 (18)	0.67 (22)	***32.9***
moving-feed (N=318)	2.1 (68)	6.0 (196)	0	1.7 (54)	0	***9.79***
moving-travel (N=1564)	12.8 (418)	30.6 (993)	3.0 (98)	1.62 (51)	0.12 (4)	***48.18***
resting (N= 166)	1.8 (58)	3.2 (104)	0	0	0	***5.11***
social (N=130)	0	4.0 (130)	0	0	0	***4***
Total *(N=3246)*	**24.4 (794)**	**63.8 (2072)**	**7 (228)**	**3.87 (123)**	**0.79 (26)**	***100***

***Note*:** the table uses the same 794 blocks (3246 scans) of adult uacaris observational data that were used to calculate time budgets. The value for N given in parentheses is for the number of scans.

The χ^2 test = 514.0 and, with 16 df, a probability of < 0.0001, showing that the distribution of activities in the various strata is not random. Almost all feeding activity in the lowest forest strata occurred in the canopy of the understory shrubs or on the ground (sections 5.3.2, 6.3.1). Although, uacaris were also seen suspending themselves by their

ankles from low overhanging branches and removing directly from the water floating macucu fruits (*Aldina latifolia*: Fab.: Caes.).

Leaping

Leaping was recorded in 4.14% of the 3791 scans of adult and non-adult uacaris in the post-habituation period (N=157). Table IV-8 gives distances (m) for 294 leaps (on- and off-scan), from this period (239 leaps by adult uacaris, 55 from smaller individuals).

Table IV-8: Observed Leap Lengths for Golden-backed Uacaris in Igapó.

Leap length (m)	***1-2***	***2.5-3***	***4-5***
No. observations - adult	89	103	47
No. observations – non-adult	53	2	0
Totals (%)	142 (48.3)	105 (35.7)	47 (16)

4.3.6 Sleeping Trees

All 43 observed sleeping trees were in igapó. Data were collected between Feb 2007 and Jan 2008. Table IV-9 displays the number of times sleeping uacaris were recorded using each of the 15 species of sleeping tree, compared with the occurrence frequency of that species in igapó quadrats. Table IV-10 shows where in the canopy they slept.

The DBH was rfecorded for 39 of the 43 sleeping trees. The mean value was 121.9cm (SD 38.19, Range 63-210), while the mean DBH for 39 trees randomly selected from the igapó quadrat data set using numbers generated at http:www.random.com (Appendix IV-1) was 52.9cm (SD 22.76, range 25-110). The trees selected as sleeping sites had a significantly larger DBH than those in the random sample (Mann-Whitney U test, $z=7.00536$, $U=1461.5$, $P < 0.001$, 2-tailed). Trees of and above the mean selected size for sleeping trees are uncommon in igapó, where they made up just 3.5% of the combined forest sample from igapó quadrat 3 and the two quadrats at the river-igapó edge (N=30/867 trees).

Of the 43 sleeping trees, 19 were within 5m of a water margin (clearing in forest or igapó/river interface), 31 were emergents, and 14 were emergents within 5m of a water margin. The emergents used as sleeping sites had a canopy that was, on average, 3.75m above the surrounding canopy (SD 1.78, range 1-8). To test statistically if the distribution of the sleeping trees differed from that of a random sample of trees, I compared the distances from the water's edge of the 35 sleeping trees for which there was data, with those of the 119 feeding trees from which I had collected a similar measurement. The mean feeding trees to waters edge distance was 84.26m (range 0-400m, SD 79.44), that of the sleeping trees was 18.25m (range, 0-50m, SD=15.81). I compared the mean distances from the river for the two classes with a Mann-Whitney U test, the results were highly significant ($z=6.42489$, $U=3487.0$, $P<0.001$).

To test if the sleeping trees were more concentrated at the forest margin simply because more large trees were present there, I compared the DBH of the 39 largest trees in the quadrats along the igapó forest edge with largest 39 trees from a quadrat (Q3) within the igapó forest. The sample from the inner quadrat had slightly larger mean DBH (128.6cm, SD=24.2) compared to the sample from the edge of the flooded forest (125.5cm, SD=23.9). However, when tested with a Mann-Whitney U test, the differences were not significant ($z=0.85444$, $U=846$, $P>0.05$, 2-tailed test), suggesting that the choice of the forest edge is not based on the prevalence of large trees there.

In addition to being larger than average, and more likely to be close to a water-forest margin, sleeping trees had other properties: compared with a random sample of 100 large (≥90cm DBH) trees in igapó; they were less likely to have lianas (N=39, 39% of random sample *vs*. N=3, 7% of sleeping trees: χ^2 with 1 d.f., 9.101, P=0.0026), all sleeping trees

lacked wasp or ant nests, though these occurred in 9 of the 100 random sample trees. Sleeping trees were also less likely than average to possess a canopy that touched that of another tree (86%, N=86, of random trees had canopies which touched other trees, while this occurred in only 16% of sleeping trees (N=7): χ^2 with 1 d.f., 19.419, P= < 0.0001).

Upon waking, uacaris were observed either to leave immediately and feed in the nearest available food tree (N=7), or to feed from the sleeping tree itself (twice), if edible items were available within it. Eating immediately upon waking was also reported for *Ateles* by van Roosmalen (1985b) and by Mittermeier (1988).

Table IV--9: Sleeping Trees – Species Identity, Frequency and Selection Ratios

Sleeping Tree Species	*No. of Records*	*% in Sleeping Tree Sample (A)*	*No. in Igapó Quadrats*	*% in Igapó Quadrats*	*Selection Ratios, B/A*
Abiurana (Pouteria gomphifolia)	1	2.32	7	0.48	4.8
Arabá (Swartzia acuminata)	1	2.32	1	0.06	38.66
Cabeçudo (Poutera elagans)	1	2.32	147	10.12	4.36
Caramurí (Eleoluma glabrescens)	3	6.97	92	6.33	1.10
Itaubarana (Acosmium nitidum)	1	2.32	13	0.89	2.6
***Louro abacatirana (Ocotea* sp.)**	2	4.64	4	0.27	17.18
Macacacaricuia (Eschweilera tenuifolia)	1	2.32	137	9.43	0.24
Macucú (Aldina heterophylla)	1	2.32	2	0.14	16.57
Piranheira (Homalium guianense, H. racemosum)	1	2.32	21	1.44	1.44
Pulero de Pato (Hydrochorea marginata)	13	30.16	59	4.06	7.42
Seringa (Hevea spruceana)	3	6.97	15	1.03	6.7
Taquarí (Amanoa oblongifolia)	5	11.6	150	10.33	1.12
***Taxí (Sclerolobium hypoleuca*)**	3	6.97	41	2.82	3.16
Tento (Ormosia paraensis)	5	11.6	14	0.96	12.08
No data	2	4.64	--	--	--

***Note*:** *data on frequency in quadrats appears in Appendix III-1.*

Table IV-10: Uacaris Sleeping Locations within Sleeping Trees

Location	*No. Records*	*% Total Records*
By main trunk (within 1 body length)	4	9.2
In crotch of large vertical branch	1	2.3
In crotch of large horizontal branch	12	27.9
On large horizontal branch (middle third)	3	6.9
On large horizontal branch (outer third)	14	32.8
At branch-twig interface	9	20.9
Total	**43**	**100**

4.3.7 Social Behaviour and Vocalizations

Social behaviour

Descriptions of feeding behaviour are presented in Chapter 5. Golden-backed uacaris at Jaú were not very social; only 4% of the observed activities involved social interaction. Social, non-feeding, behaviour is treated qualitatively and details are presented in Appendix IV-2.

Grooming: Social grooming occurred at a very low frequency, being observed just 12 times, with all observed instances occurring between adolescents (Appendix IV-2).

Aggression: Aggression between group members was rare, being observed only four times. In each case this appeared to be a mother reacting defensively towards perceived threats to her presumed offspring (Appendix IV-2). No direct aggression by males was ever observed. However, on one occasion, a band became very agitated upon hearing the calls of another uacari band from which it was separated by a branch of the Rio Jaú (Appendix IV-2). Probable male animals (slightly larger, with slimmer waists) made the majority of the responding calls and reactions. Bezerra *et al*. (in press) report incidents of fighting between uacaris at Jaú, but acknowledge that these were rare. I personally observed no such events. Neither did I observe the displacement or submissive calls, or submissive behaviours, as permeate other primate societies (e.g. Aureli & Schaffer, 2007 for *Ateles*; Matheson *et al*., 1996 for *Cebus apella*; Whitham & Maestripieri, 2003 for *Papio cynocephalus*; Aureli *et al.*, 2002 for review)

Play: Play was not observed in adult animals. All observations involved sub-adults and juveniles. In the case of some juveniles, they devoted so much time to chasing each other that I never saw them suckle or feed (Appendix IV-2).

Other behaviours: A single sexual display was observed (by a young male). Threat displays were observed being given to *Cebus albifrons*. I did not observe any mating, but this behaviour at Jaú is reported by Bezerra *et al.* (in press). A single branch-breaking display was directed against human observers. Observers were defecated on once. Details of these various behaviours are given in Appendix IV-2.

Feeding together

This was not commonly observed. Table IV-11 presents the number of feeding trees in which between one and five weaned or adult uacaris were recorded feeding simultaneously in the same food patch (292 scans). Because they were not feeding on the fruit, but merely present on their mother's backs, dependent infants were excluded from this analysis and not included amongst the counts of the number of foraging individuals. Despite group sizes of up to 40, no more than 5 animals were ever recorded together.

Table IV-11: Frequency of Co-feeding in Same Food Patch

	No. Uacaris				
	1	***2***	***3***	***4***	***5***
No. Observations	*228*	*38*	*19*	*5*	*2*
% of Total Feeding Observations (N=292)	*78.1*	*13*	*6.5*	*1.7*	*0.7*

Vocalizations

Table IV-12 presents data on eleven vocalization types and their perceived contexts. I did not observe mating behaviour in golden-backed uacaris. This is reported by Bezerra *et al.* (in press), a paper which also categorizes types of uacari locomotion. A number of other calls were heard while observing, but as these were not from the focal animal the

behavioural context is not known. These included a deep harsh '*Rarrk'*-like call that may have paralleled the *Rhork* and *Rhä* calls reported for *C. c. ucayalii* (Fontaine, 1981; Bowler, 2007), and which are associated with male-male aggressive encounters.

Table IV-12: **C. m. ouakary** ***Vocalizations and their Contexts***

Call	***Situation***	***Presence of similar call in other uacari species?***
Twitter	A near-constant accompaniment to uacari movement. Heard daily	Reported as *Hic* by Fontaine (1981) and Bowler (2007) for *C. c. ucayalii* and as *'ca-ca-ca-ca'* for *C. c. calvus* (Ayres, 1986a). *Keeks* and *Chicks* by Boubli (1997a) for *C. m. melanocephalus*
Trill	Lower frequency and more staccato version of twitter. Uttered during some (not all) of the occasions when one adult animal approached (too close to?) another. Heard on four occasions.	Possibly equal to the 'soft *chick*; calls reported by Bowler (2007).
Cough	A plosive '*Pof*' or '*Bof*' made at end of Trill sequence. Heard on three occasions. Significance unclear.	
Chok	Moderate alarm, one or two choks by an individual rarely elicited notable response from other band members, but if persisted would cause pausing and head turning. If more than two animals began *chok*calling, flight was often the response. Flight was usually not accompanied by calls. Heard almost daily	Reported, as *Chyook* by Fontaine (1981) and Bowler (2007) for *C. c. ucayalii.* Often heard during bouts of aggression.
Screech-chok	Sucking noise precedes the 'chok'. Higher level alarm.	
Cheng	Metallic more vigorous version of Trill. Trill-Chok-Cheng form a graded series of increasingly intense emotion.	Reported, as *Chick* by Fontaine (1981) and Bowler (2007) for *C. c. ucayalii.* Often heard during bouts of aggression. Also given, as the 'strong *chick*' as an alarm call for birds of prey.
Bi-co bark	Loud two-syllable bark-like vocalization, given in extreme and immediate danger (such as sudden appearance of diving raptor). Appears to be given only by largest adults. Heard on a regular basis.	

Table IV-12: Vocalixations – continued 1		
Call	*Situation*	*Presence of similar call in other uacari species?*
Ko-ko	Very quiet call sometimes given by adults when feeding. Heard six times (probably more common but low decibel level made the call hard to hear)	
Scream	Given by young and juveniles while playing. Almost always heard when animals played. Sometimes accompanies by *cheng*-like chatters.	*Scream* (Bowler, 2007), *Kreek* and *Wa* (Fontaine, 1981). Given by infants and juveniles when stressed.
Hiss	Given by young when close to mother (only heard twice, probably due to low decibel level of call). Significance unclear.	Reported for juveniles by Boubli (1997a).
Toc	Given by mother when trying to attract free-ranging infant to her side. Number of calls increased with urgency, to diads and triads, and increasing stridency the longer the infant delayed response. Heard on seven occasions. Sounded like a muttered 'chock' call.	

4.3.8 Interactions with Other Species

Uacaris and other primates

Eight other primate species are known in Jaú (red howler, *Alouatta seniculus*; night monkey, *Aotus trivirgatus*; white-fronted capuchin, *Cebus albifrons*; tufted capuchin, *Ce. apella*; golden-headed saki, *Pithecia pithecia chrysocephala*; mottle-faced tamarin, *Saguinus inustus*; golden-handed tamarin, *Saguinus midas*, and squirrel monkey, *Saimiri sciureus*: Barnett *et al*., 2002). Only *S. inustus* was not recorded in the current study.

Table IV-13: Habitat Records for Other Primate Species Recorded During the Study

Species	***Habitat Type***	
	Igapó	***Terra firme***
Alouatta seniculus	X	XX
Aotus trivirgatus	X	--
Cebus albifrons	XX	X
Cebus apella	--	XX
Pithecia p. chrysocephala	X	X
Saguinus midas	--	X
Saimiri sciureus	XX	XX

(X = recorded during study, XX = recorded each month)

Uacaris were very rarely seen for more than a few minutes in close proximity to other primates. The few instances on which this occurred are documented in Appendix IV-3. Bezerra (in prep.) also reports interactions between *C. m. ouakary* and *Aotus trivirgatus,* a species not seen by me. On at least seven occasions, I heard contact calls of *Cebus albifrons* groups, while watching uacaris in the igapó. The calls elicited no obvious response from the uacaris.

Uacaris reactions to large birds and arboreal non-primate mammals

During field observations, uacaris were recorded in proximity to 46 types of vertebrates, of which 38 could be identified with certainty to species. Appendix IV-4 presents descriptions of uacari behaviour during encounters with these other arboreal mammals and reptiles, and passerine, psittacine and raptorial birds. Of the 245 encounters, 191 (77.9%) resulted in no observable reaction, 31 (12.6%) in threat-avoidance behaviour that lasted for minutes and could have strongly interrupted foraging. Twenty reactions were of mild short-lasting alarm (8.2%), and three (1.2%) encounters initiated investigation (discovery of a frog and two small lizards). Of 31 events where strong reactions were elicited, 25 (80.6%) involved raptors flying within 5m of uacaris or calling close by. Raptors flying at distances ≥15m from uacaris (22.8% of all encounters and 69.1% of observed encounters with raptors) elicited no discernable reaction.

Raptor Surveys

During 53 days across Jan-May 2007, raptor species capable of capturing a uacari were recorded at a mean rate of 1 every 58.50 hrs. Over this period, raptors (including vultures and caracaras) to which uacaris reacted with alarm calls (bico-bark) were encountered at a mean rate of 1 every 5.25 hrs. The presence of such birds often caused a cessation of feeding and calling, for up to 7.5 mins. after contact. This, plus the associated influences

of risk-sensitive foraging (Miller, 2002) can have an important impact on the time-budgets of primates (Di Fiore, 2002).

4.4 Discussion and Conclusions

4.4.1 Activity Budgets

Table IV-14 compares activity budgets from the current study with those from other members of the genus *Cacajao* and other large Neotropical primates.

Table IV-14: Published Activity Budgets for Larger Neotropical Primates

Species (wt.-diet)	***Travel***	***Feeding***	***Resting***	***Social***	***References***
Cacajao m. ouakary	**42.8**	**48.1** [1]	**5.1**	**4**	**current study** [2]
Cacajao calvus calvus	35	36	29	---	Ayres (1986a)
Cacajao calvus ucayalii	39.2	31.7 [3]	24.4	5.8	Bowler (2007)
Cacajao m. melanocephalus	27	51 [2]	22	---	Boubli (1997a)
Alouatta belzebul	18.2	20	57	3.1	Pinto (2002)
Alouatta palliata	15.6	13.4	66.2	4.8	Milton (1980)
Alouatta pigra	9.8	24.4	61.9	(3.9) [4]	Silver *et al.* (1998)
Alouatta seniculus	12.7	5.6	78.5	3.2	Gaulin & Gaulin (1982)
Ateles belzebuth	22.2	14.8	63	---	Klein & Klein (1977)
Ateles chamek	18.9	29.7	45.5	5.9	Wallace (2001)
Ateles geoffroyi	27.6	10.8	54	7.3	Richard (1970)
Brachyteles arachnoides	29	19	49	3	Strier (1987)
Cebus albifrons	21	66	18	1	Terborgh (1983)
Cebus apella	21	61	12	1	Terborgh (1983)
Cebus olivaceus	20	45	22	13	Robinson (1986) [5]
Chiropotes satanus satanus	58.5	19.8	13.8	7.9	Port-Carvalho & Ferrari (2004) [6]
Lagothrix lagotricha	38.8	25.8	(11) [7]		Defler (1995)
Lagothrix poeppigii	34.5	34.5	23.2	6.1	Di Fiore & Rodman (2001)

Notes:
1 combines categories for paused feeding and feeding while moving
2 'feeding' combines feeding when paused and when moving, 'moving' refers to travel only
3 combines Bowler's categories of 'feeding' and 'searching foliage'
4 calculated from figures in text, not given by authors
5 figures for adult males, derived from Figure 12, p. 28 of Robinson (1986).
6 from a population in a forest fragment
7 resting and other not separable from data in text, 11% of time budget therefore remains unallocateable.

Comparing observed time allocations of Jaú's golden-backed uacaris with those presented for other flooded-forest-inhabiting *Cacajao, C. c. calvus* and *C. c. ucayalii*, it appears that, like *C. m. ouakary*, the latter devote roughly equal time to travel and feeding. In addition, like *C. m. ouakary*, social behaviors occupy a very small percentage of the time of *C. calvus* uacaris, compared to species like *Ce. apella*. As with members of predominantly frugivorous genera like *Ateles* and *Lagothrix*, all members of the genus *Cacajao* studied so far spend a very high proportion of time travelling when compared to such predominantly folivorous forms as *Alouatta*. The amount of time spent resting by *C. m. ouakary* is remarkably small compared with all other studies in Table IV-14 except Defler's 1995 study of woolly monkeys. Unless it is the consequence of natural timidity or an artifact of incomplete habituation, this would place golden-backed uacaris at the extreme end of the ''energy-maximizer/time-minimizer'' continuum. This is consistent with golden-backed uacaris habit of foraging while on the move, where individuals were often seen moving tripedally holding or eating a food item. The closest relative of *C. m. ouakary, C. m. melanocephalus*, is also known to do this a significant proportion of the time, with Boubli (1997a) recording 31% of the daily time budget as ''moving/foraging''. The summed annual value for moving/foraging in *C. m. ouakary* is 58% (moving feed, 9.9%, plus moving travel, 48.1%: Fig. IV-2). However, in the current study, no full-day follows were ever achieved, and the possibility must be accepted that uacaris rested in those times during the day when they were not observed.

Aureli *et al*. (2008)'s proposed heuristic revisioning of the terminology of primate fission-fusion dynamics involved three components: i) temporal variation in band member spatial cohesion, ii) temporal variation in party size, and iii) temporal variation in party

composition. Though data for (iii) are lacking for uacaris in general, the known extent of (i) and (ii) in *Cacajao*, including *C. m. ouakary*, places the members of the genus in Aureli *et al*.'s (2008) 'higher FF' category. As noted by a number of authors (e.g. Anderson *et al*., 2002; Asensio *et al*., 2008, 2009; Kappeler & van Schaik, 2002; Lehman *et al*., 2007), fission-fusion sociality is a strategy for reducing competition for food between band members and also reducing the mean between-patch distance that must be travelled. However, the fluid nature of the society means that social bonding tends to be less in species that fall into Aureli *et al*. (2008)'s 'high FF' category (Aureli *et al*., 2008; Emery-Thompson & Wrangham, 2006; Kappeler & van Schaik, 2002).

In uacaris, the notable lack of social interactions may be associated with their fission-fusion sociality and the consequent lack of frequently reinforced social bonding (Bowler, 2007; Bowler & Bodmer, 2009), though it should be noted in this context that other fission-fusion species (e.g. chimpanzees) have substantial proportions of their time budget devoted to social behavior (e.g. Doran, 1997; Matsumoto-Oda, 2002; Matsumoto-Oda & Oda, 1999). This might be partially explained by the presence of extensive individual variation in call tones (Mitani *et al*., 1996), pelage colour and facial shape (Bauer & Philip, 1983), and markings all of which are considered to aid individual recognition (Parr & de Waal, 1999),. This may well facilitate social interactions. In contrast, the lack of individual markings in golden-backed uacaris might act as a very real barrier to the development of such structured events.

The small proportion of the recorded *C. m. ouakary* activity budget devoted to resting, (5.1%) is considered to be a partial artifact. As seen in Table IV-3 and IV-4, resting was not recorded in three of the months for which time budget data were collected. This drew

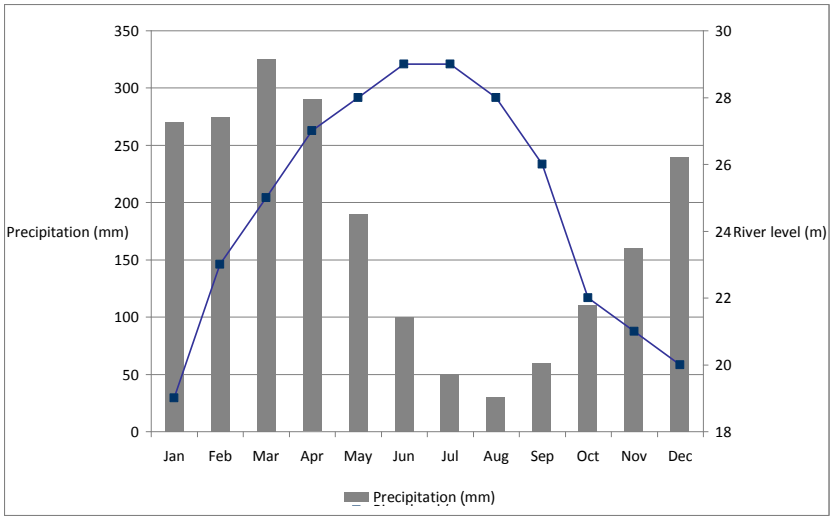
down the average to the low level in the table, and would have consequently raised values for other behaviours. For the six months in which it was recorded, resting varied between 5.8 and 8.8% (mean 7.55%). Though there appeared to be a regular, but short, rest period between the hours of 09.00 and 10.00, this percentile is still far below those in the time budgets of other frugivorous Neotropical primates (Table IV-14). Further discussion of time budgets occurs in the context of foraging and food availability in Chapter 6.

4.4.2 Reproduction

Timing of reproduction

Theories concerning optimization of reproductive investment as part of a life history strategy that maximizes overall reproductive success (Charnov & Schaffer, 1973; Cohen, 1971; Cole, 1954) predict that animals time births to maximize survival changes of offspring. As uacaris live in a strongly seasonal environment, such theories predict that uacari births should occur non-randomly across the year. Very young infants were recorded in two distinct annual periods (Dec and May: Section 4.4.2), suggesting some level of birth seasonality. Female *Alouatta*, *Cebus* and *Saimiri* were also seen carrying small infants in Dec 2006, indicating this may be a general pattern in Jaú's primate community. As shown in Fig. IV-4, Dec is in the middle of the rainy season at Jaú. In terra firme it is a period when both fleshy fruit and maturing leaves are at a maximum in central Amazonian terra firme forests (e.g. Alencar *et al.,* 1979; Haugaasen & Peres, 2007a; Parrado-Rosselli *et al.,* 2006). Timing of births in many Amazonian primates appears to be timed to avoid the stress of the dry-season fruit dearth (Haugaasen & Peres, 2007b; Peres, 1994a,b). Though folivores tend to have less clumped birthing periodicity than frugivors (Di Bitetti & Janson, 2000), it is possible that *Alouatta* at Jaú, may, by avoiding mature leaves whose detoxification and digestion are energetically demanding

(Kowalewski & Zuninho, 2004), be reducing energetic stress on parenting females (Iason, 2005). As observed by Crocket & Rudran (2005), such timing in *Alouatta* may also maximize availability of weaning foods later the following year. Similar factors may be influential in determining breeding times of more generalist species such as *Cebus* and *Saimiri*, where infants wean at 9 and 6 months (Wilen & Naftolin, 1978; Defler, 2004), respectively. Such timings would place weaning in the dry season. In central Amazonia this is the season when caterpillars and other folivorous insects feeding on flushing leaves are most abundant (e.g. Veiga & Ferrari, 2006), and insects often more strongly represented in the diet of post-weaning *Cebus* and *Saimiri* than other ages (e.g. Stone, 2008: *Saimiri sciureus*). This may be especially pertinent given that the ontogeny of manual dexterity and coordination required to effectively catch and process arthropods does not occur immedialtly after weaning (e.g. Hopf & Ploog, 1991: *Saimiri*), delaying the time when microcarnivory can be effective as a contributor to an energetically optimized diet and further focusing selection for resource-predicated timing of parturition in primates. The time required for the digestive tract to modify morphologically and chemically to accomodate the adult diet (Langer, 2003: general review of this topic for mammals) must also be considered.



after Ferreira (1997)

Fig. IV-4: Rainfall Distribution and River Water Levels on the Middle Rio Negro

In a review of patterns of birth seasonality in Neotropical primates, Di Bitetti & Janson (2000) identified three alternative birth strategies that were followed: i) reduce energy stress during peak lactation; ii) wean infants during peak food availability; iii) store reserves during peak energy availability. In addition, primates must strive to give birth at a time that allows peak infant growth and peak food availability to coincide. At the time of Di Bitetti & Janson's paper, Ayres (1986a) was the only source of data on breeding periodicity in the genus *Cacajao.* Noting that reproduction in this species is shortly before the peak of fruit and new leaves, Di Bitetti & Janson placed uacaris in their A1 category, where optimization of reproductive effort in relation to energy availability involved minimizing energetic stress on the mother during peak lactation. This may also be the situation for female *C. m. ouakary* at Jaú.

At Jaú, the birth of babies in Nov would allow the dam to support the costs of lactation and carrying the infant during the part of the year when foods are most available (figs. III-10 and III-11, Section 3.4). This pattern of investment is common in primates (e.g. Di

Bitetti & Janson, 2000; Van Schaik & Van Noordwijk, 1985). Based on the observation that mortality in young primates is often highest in those months immediately following weaning, when young animals have to learn to apply foraging and food processing rules, while still lacking both the manipulative skills (e.g. Fragaszy & Adams-Curtis, 1997), and the full physical force that may assist adults in their own food finding (Young, 2005), Janson & van Schaik (2000) emphasized that a key factor is the timing at which weaning occurs. Since they have less well-developed foraging skills than adults, newly-weaned or recently-weaned individuals may well be more adversely affected by downturns in resource availability that occur in this period.

Temporal spread of reproduction

The records at Jaú of very young infant *C. m. ouakary* in Dec concord with a single observation (reported in Defler, 2004) of a Nov birth for this species in Colombia. The infants observed in Dec were not beyond Fontaine's Stage *'Infant 1'* (10-20% of mother's size, little locomotor competence: Fontaine, 1981), which, if developmental speeds are the same in *C. m. ouakary* as for *C. c. ucayalii*, would mean that birth had occurred no more than 3 months before. At Jaú, mating, though not seen during the current study, has been observed in May (Barnett, 2005; Bezerra *et al*., in press). Given the size of *C. m. ouakary*, a 6-month gestation period might be expected (Lindburg, 1982), which would also accord with Nov birth data. The second period of mating has not yet been observed, but if the two-peak breeding cycle is real, then this might be predicted to occur in Nov, for babies to be born in May. A two peak breeding cycle does not accord with the very tight reproductive season predicted from Dixson & Anderson's (2002) studies of genital morphology. Based on penis length and morphology and the relative size of the testes, Dixson & Anderson placed members of the genus *Cacajao* in the category of primate

species where male-male competition is intense, but nonphysical, and based instead on sperm competition. This occurs in species where breeding occurs only in a very narrow time window, often due to the strongly seasonal nature of reproduction. It must be considered that the Dixson & Anderson model is correct, but that it should be expanded to allow intense competition to occur in two widely spaced parts of the annual cycle. Bowler (2007) reported *C. c. ucayalii* to be a seasonal breeder, with all births either observed or inferred to occur between Aug and Nov. August marks the beginning of the period of fruit abundance at Bowler's Lago Preto site.

4.4.3 Distances Between Individual Uacaris

All previous detailed long-term studies of uacari taxa (Ayres, 1986a,b; Boubli, 1997a; Bowler, 2007) have reported that they travel in large groups in which the individuals are generally widely dispersed. As Table IV-15 shows, the nearest-neighbour distances for adult golden-backed uacaris are within the range of other primate species, but greater than those published for most other Neotropical primates of a similar size.

Table IV-15: Nearest Neighbour Distances of Large, Diurnal, Non-generalist Primates

Species	*Nearest Neighbour Distances (m)*	*Reference*
Cacajao m. ouakary: **adult male**	**5.5 (mean)**	**Current study**
Cacajao m. ouakary: **unsexed adult**	**4.3 (mean)**	**Current study**
Cacajao m. ouakary: **adolescent**	**2.8 (mean)**	**Current study**
Alouatta palliata[1]	≤ 3m (60.7% of time)	Rodrígues (2007)
Brachyteles sp.	< 1m (30% of time), <5m (50% of time)	Strier (1992)
Cebus capucinus: adult males	< 2m (48% of time)	Oleson & Foufopoulos (2007)
Cebus capucinus: adult females	< 2m (55% of time)	Oleson & Foufopoulos (2007)
Cebus capucinus: juveniles	≤ 2m (60% of time)	Olsen & Foufopoulos (2007)
Lagothrix poeppigii	< 2m (high % of time budget, ≤ 5m (48% of time)	Di Fiore (2002), Di Fiore & Fleischer (2005)

Table IV-15: Nearest Neighbour Distances (contd.) – 1

Species	*Nearest Neighbour Distances (m)*	*Reference*
Pan paniscus	5.5 m (mean)	White & Chapman (1994)
Pan troglodytes	4.1 m (mean)	White & Chapman (1994)
Propithecus diadema	≤ 5m (64-68% of time)	Irwin (2007)

Table IV-6 shows that uacari associations are themselves diffuse, with 75.16% (N=112) of band spreads exceeding ≥101m. Moreover, the sub-groups that forage in the same area are also widely separated. Mean distance between sub-groups simultaneously visible to me was 116.6m, though the presence additional out of sight animals could mean this value is somewhat conservative, as foraging units that operate in the same area may also be widely separated. Ayres (1986a) believed that foraging units of a *C. c. calvus* band could be spread over several kms.

This type of diffuse presence is typical of fission-fusion foragers (Chapman, 1990a,b; Aureli *et al*., 2008), and is an adaptive response by such primates to a combination of extended distances between suitable foraging patches, the size and depletability of such patches and the existence of small sized foraging parties to reduce resource competition among band members (Norconk & Kinzey, 1994). This strategy contrasts strongly with that of other members of the Jaú primate community, such as *Alouatta seniculus, Saimiri sciureus* and *Cebus albifrons.* For these species, I observed band spreads to be as little as 10m for a group of 27 *S. sciureus* and 15m for eight-strong groups of *Ce. albifrons*, while group spreads for *Alouatta seniculus* rarely exceed 20m for an entire 6-10 strong group. Many of the *Cebus* and *Saimiri* could be identified individually and were known to have inhabited the areas being surveyed throughout the uacari study. Hence, it is presumed that

such data reflects behaviour that is not a fright response to the presence of an observer, and that such small group spreads were not abnormal.

4.4.4 Use of Forest

Use of vertical space in the forest – emergents, canopy, sub-canopy, shrubs and ground

Energetic considerations: The great majority (88.2%) of observed uacari activity occurred in either emergent trees or the forest canopy. When in emergents, uacaris spent proportionately more time in moving travel than any other activity, although the actual proportion of time uacaris spent in moving in emergents was less than that spent in moving-travel in canopy (12.8% *vs*. 30.6% of all activity and 56.2 *vs*. 47.9% of values for, respectively, emergents and canopy alone). The canopy stratum was the focus of 63.8% of all recorded activity (88.3% when emergents and standard canopy are combined). Sub-canopy was rarely used (7 % of scans), and visits were mostly to feed in small trees such as *Mouriri* sp. (Memcylaceae), and smaller individuals of *Duroia velutina* (Rubiaceae). This skew in stratum use can be attributed partly to the comparatively greater volume of food in the canopy, partly due to the broken nature of the understory and sub-canopy, and partly due to the way in which uacaris move. Igapó has a very sparse understory and a sub-canopy that consists of widely-scattered small trees and palms (Fig. II-4). Unless the uacaris were to swim regularly, accessing these resources when the forest is flooded requires horizontal movement within the canopy of taller trees, and then a descent (often by dropping) into the leaves and branches of a sub-canopy or understory tree. Post-feeding, this must be followed by an ascent into the canopy if another tree or palm in the understory or canopy is to be accessed. This crenellation-like progress occurs because *Cacajao* lacks the skeletal specializations required to perform the vertical-clinger-and-leaper form of locomotion characteristic of *Pithecia* (Fleagle & Melrum, 2005), which

allows these close relatives of uacaris to exploit terra firme forests understory and sub-canopy (Norconk, 2007; Walker, 2005). In *Cacajao* the limb morphology and locomotory behaviour appear poorly adapted for horizontal locomotion within the sub-canopy, and the greater energetic investment required by the resulting ascend-along-descend format could probably be repaid if the target canopies were large with ample crop volumes. However, all fruiting understory and sub-canopy plants observed in Jaú's igapó had small canopies, small absolute crop volumes, or both (Table III-9, Section 3.5). In addition, the mean distance between understory or subcanopy trees or shrubs that were of fruit-bearing age is 21.3m in igapó and 9.4m in terra firme, while the mean distance between canopy trees in the two habitats is 3.1m and 5.7m, respectively. Hence, distance between understory and sub-canopy trees is greater in igapó than between canopy trees, making it very probable that the energetic yield from exploiting these resources is less than exploiting those of the canopy. It might be predicted that the only time that it would become optimal to exploit understory and sub-canopy trees is when fruit available there exceeds that available in the canopy. This prediction will be tested in Chapters 5 and 6.

Competition: In addition, it should be noted that while observed patterns of habitat use may have bases in physiological and morphological explanations, the role of competition should not be ignored. The only two other primate species that were regularly encountered in igapó were *Cebus albifrons* and *Saimiri sciureus.* Both species were more frequently encountered in the middle and lower strata than in the upper, observations which accord with what has been recorded about their ecology elsewhere in Amazonia (e.g. Baldwin & Baldwin, 1981; Defler, 2004; Fragaszy *et al*., 2004; Kinzey, 1997; Terborgh, 1983). Both are known to be more generalist feeders than *Cacajao* (ibid.), and so it is likely that they

would exploit throughout the year many of the resources (insects; ripe small and succulent fruit) that uacaris would ignore. Moreover, they would do this at the lower canopy levels, levels which, it seems, uacaris enter only in the extremetis of a dry season fruit dearth. Thus, if competition *is* occurring, then it is likely to be doing so only very seasonally and, even then, the leaf-and-pith-dominated diet that uacaris have at this time (Chapter 5) may further minimize the effective dietary overlap.

Uacaris and terrestriality

Ayres (1986a) observed *C. calvus* foraging on the floor of unflooded várzea, where they ate unidentified germinating seedlings (from the written description of the seeds, I believe they were probably Sapotaceae). At Jaú, golden-backed uacaris were not observed to descend to the ground to travel, only to feed on germinating seedlings (Section 5.4.5), with all below-canopy and sub-canopy travel registered in the study occurring in low shrubs (mostly Myrtaceae). Groups observed foraging on the ground were never more than five animals strong. To forage on the ground, *C. m. ouakary* was seen to descend quickly from an overhanging branch and then either to grab a handful of germinating seedlings and go back to the perch, or to sit on a buttress root and eat them. However, observations of large patches of seedless stalks on open ground indicate that uacaris do sometimes spend time feeding on the ground itself. Partially-eaten seeds all bore characteristic marks of uacari teeth, so it is considered most likely that only uacaris were engaged in this activity, and no other primate. Other high-canopy Neotropical species, such as *Ateles*, have been observed to come to the ground to eat soil, to drink and to eat rotting wood (Campbell *et al.*, 2005; Dew, 2005; Izawa, 1993). Though they have yet to be observed to do so, *C. m. ouakary* may use the clay of arboreal termite mounds as has

been reported for other pitheciine genera (Setz *et al.*, 1999 for *Pithecia* and Veiga & Ferrari, 2007 for *Chiropotes*), but not for *Cacajao* (Ferrari *et al*., 2008). Peruvian red uacaris drink from bromeliads and tree holes (Bowler, 2007). This has not been observed for *C. m. ouakary*, but Bezerra (unpublished data) reports an incidence of an animal suspending itself from a branch to drink from the river surface.

Use of rotten wood as a supplemental source of elements (principally phosphorous), and not as a source of wood-boring grubs (but see the 'microcarnivory - larvæ within dead wood' portion of Section 5.4.5, p.289), has been reported for several primates (e.g. mountain gorillas: Rothman *et al.*, 2006; spider monkeys; Felton *et al*., 2008). In Jaú, local guides reported that *Alouatta* and *Cebus* came to the ground to feed on rotting wood, though I saw only the latter. There appear to be no previous records of dead or rotting wood use for the genus *Cacajao.*

4.4.5 Sleeping and Sleeping Trees

Sleeping trees are being reappraised as an ever-more significant aspect of the ecology of primates (Anderson, 1998), and their distribution can have strong influences on ranging patterns and foraging decision (e.g. Day & Elwood, 1999 for *Saguinus midas*; van Roosmalen, 1985b for *Ateles p. paniscus*), as well as being a key defence against nocturnally-active predators (Chapman, 1989 for *Ateles geoffroyi*; Di Bitelli *et al.*, 2000 for *Cebus apella*). Primates are often highly selective of their sleeping sites, sometimes choosing very specific tree species that maximize predator protection, comfort and social contact (e.g. Heymann, 2009 for *Saguinus mystax* and *Saguinus fuscicollis*; Radespeil, 1998 for *Microcebus murinus*; Zhang, 1995 for *Cebus apella*), and have a low probability of branch loss under windy conditions (Di Bitetti *et al.*, 2000). While some species use many different sites, and may rarely use the same trees (e.g. Chivers, 1969: *Alouatta*

palliata; Lindburg, 1971: *Macaca mulatta*; Ramakrishnan & Coss, 2001: *Macaca radiata*), others will re-use the same sleeping trees for successive nights, sometimes for months (e.g. Chapman, 1989; Rasoloharijaona *et al*., 2003: *Lepilemur edwardsi*), or even years (e.g. Mertl-Millhollen, 2000: *Lemur catta*). Other species alternate between a series of defined localities (Chapman, 1989; Di Bitetti *et al.*, 2000). At Jaú, uacaris rarely slept in the same general area twice and were never recorded re-using sleeping trees.

The nature of sleeping trees has not been recorded previously for either *C. calvus* or *C. m. melanocephalus*, with neither Ayres (1986a), nor Boubli (1997a), respectively, giving any details on sleeping sites for their study uacaris. Bowler (2007) also gives little information other than to say that after a diurnal resting bout, 45 *C. c. ucayalii* were counted as leaving a single tree. However, other, shorter, studies have provided some observations on uacari sleeping trees. Aquino (1995b) noted that sleeping trees always exceeded 20m in height, and Aquino (1998) reported that sleeping sites were mostly in the crowns of trees from 17 to 32m tall. Troop members did not sleep together in one large group, but were distributed between appropriate trees across an area of up to 2ha in extent, with 6-7 animals in each tree (Aquino, 1998). Such trees were primarily of *Pouteria* and *Eschweilera* spp. Following a troop of some 80 *C. c. ucayalii*, Swanson-Ward & Chism (2003) noted that the monkeys stopped moving around 17.50 and were settled for the night by 18.00. The group had scattered into a variety of trees, of which two (an *Eschweilera*, and a *Mimosa* [Fab.: Mim.]) were occupied at a height of some 25m. For *C. m. ouakary*, Defler (2004) reported that, around Lake Taraira, on the lower Río Apaporis, Colombia, groups of sleeping golden-backed uacaris in flooded igapó occurred on the ends of large strong branches in leafless canopy, up to 15m above the floodwaters, while

in non-flooded terra firme forest they chose trees with a much higher (25-30m) and less-exposed canopy.

All observed sleeping trees were found in igapó. I was unable to track uacaris to their night-time resting places when they were in terra firme, so it is currently unknown where uacaris sleep during those months. However, in 2000 I made a near-dusk observation of a band of some 100 uacaris heading from terra firme to igapó, so it is possible that they continue to use igapó as a dormitory during this time. This might be aided by the apparent fact that uacaris at Jaú rarely venture more than 0.5km from the igapó/terra firme ecotone (Barnett *et al.*, 2005; S. Iwanaga, pers. comm.; C. Peres, pers. comm.). This is not, however, the case at other localities. For example, at Camurú in Colombia, Defler (1999) reported *C. m. ouakary* up to 5km into terra firme (Barnett *et al*., in press). T. Defler (pers. comm.) reports that the uacaris were there for several successive days.

For species with sleeping trees in unflooded forests, presence of fæces and seeds under their canopies makes it possible to be certain that sleeping trees are repeatedly used even the absence of observations to that effect (e.g. Chapman, 1988a). This is not possible with uacaris, where such debris are washed away by the current. This natural sanitation makes it very unlikely that parasite avoidance as a prime mediator of sleeping site selection (e.g. Gilbert, 1997; Hamilton, 1982; Hausfater & Meade, 1982) is applicable in the case of uacaris. Under such circumstances predation avoidance is the most likely factor influencing choice of sleeping tree.

Repeat usage and choice of sleeping sites

Though uacaris were not recorded using sleeping trees more than once, it is possible that, like *Ateles geoffroyi* studied by Chapman (1988), they may have returned to the same trees after several days absence and have a series of very widely spaced trees that are used

whenever the animals are in a particular area, rather than using trees on a single occasion. This view is supported by the particular nature of the trees in which golden-backed uacaris choose to sleep (below), plus the fact that they rarely sleep more than three to a tree. However, as a group, they do sleep in several trees near to each other. As sub-groups tend to join up at night, this would mean that many trees would be required to support a group of 15-40 animals. Chapman (1988a,b) noted that *A. geoffroyi* sub-groups also tended to fuse prior to entering sleeping sites. He also noted that sub-groups appeared to be coordinated by the use of the species' inter-group contact call. No such calls were ever heard whenever uacaris accumulated at Jaú. Indeed, *C. m. ouakary* were notably quiet once in their sleeping trees, with very few of the otherwise almost incessant *twitter* and *chock* calls being heard. Bowler (2007) also noted this quietitude in retiring *C. c. ucayalii.*

Selection of tree types as sleeping trees

As shown in Table IV-9, *C. m. ouakary* exhibits preferences for tree species in which to sleep, with *Hydrochorea marginata* (Fab.: Mim.) being by far the most frequently used. The properties of the canopy of this tree (broad, open canopy with clean horizontal limbs and a branching pattern provides an uncluttered canopy interior) appear to be attractive to a variety of wildlife. The regional name, *Pulero de Pato*, means 'Duck Roost' and, indeed, these and other broad winged birds (such as herons, ibis and large parrots) were frequently seen roosting in its canopy. It has the second-highest selection ratio for uacaris any of the tree species for which multiple records were obtained, being used at a frequency that is sufficiently disproportionate to its frequency in the forest to suggest very active selection by uacaris. The species with the highest selection ratio, *Ormosia paraensis*, also has this canopy type. It is possibly significant that both have compound leaves with small leaflettes, which would enhance visibility from within the canopy, and assisting in the

detection of potential predators. For *Ateles*, Mittermeier (1988) notes that preference seems to be given to trees that are small leaved or to leafless canopies. Selected sleeping trees are often broad with many wide horizontal branches (Mittermeier, 1988 for *Ateles*; Di Bitetti *et al.*, 2000 for *Cebus*).

The trees in which sleeping occurs are statistically significantly larger than the average igapó tree. This may indicate strong selection by uacaris for larger trees. In addition, as data in Section 4.3.6 indicate, the uacaris appear to demonstrate a distinct preference for large diameter, emergent trees. This form of preference is commonly recorded wherever primate sleeping habits have been analysed (e.g. Hamilton, 1982, Wahungu, 2008 for baboons; Di Bitetti *et al*., 2000 for *Cebus*; Anderson, 1998 for review). As such trees provide vantage points from which aerial predators might best be seen and are the furthest distance possible from the ground (and its predators), the use of emergent trees is generally considered to be a predator avoidance strategy, or a means of getting as much warning as possible of such an animal's impending arrival. In addition, uacaris select trees that tend to have smaller leaves (and hence better visibility for disturbed primates), are close to open water, and lack both lianas and crowns that touch those of neighbouring trees. In selecting their sleeping sites, the uacaris also appear to have avoided trees that had wasp and ant nests. All but the latter could most parsimoniously be interpreted as choosing trees that offered the highest protection against nocturnal arboreal predators. Whilst increased nocturnal visibility might also be considered an aid to predators, most Cebid primates are at a visual disadvantage at night and choosing a site from which, once alerted to the presence of a predator, they would have the best chance of seeing what it

was doing and working out how to avoid it, may strike the best balance between seeing and being seen.

In addition (Table IV-10), the location in which the majority (52.3%) of animals chose to sleep (the outer third of large horizontal branches and the branch-twig interface) might also be seen as the best compromise between avoiding attacks by both arboreal and aerial predators. Ramakrishnan & Coss (2001) found a similar situation in both Hanuman (*Semnopithecus entellus*) and Nilgiri langurs (*Trachypithecus johnii*), noting that by sleeping alone and away from the main trunk of horizontal branches, the langurs avoided heavier arboreal predators such as leopards.

The combination of size with other apparently favoured characters, *viz.* proximity to water, absence of lianas or wasp nests, requires a suite of characters that are probably rarely met, and will co-occur at just a few sites, even within a range as extensive as a uacari troop's. It seems unlikely that trees bearing these suites of specific attributes could be encountered reliably at the end of each day's foraging. Therefore, it is posited that uacaris probably rotate through a series of specific sleeping sites, as do the *Ateles* studied by Chapman (1988). As uacaris do not seem to use the same sleeping site for several nights in succession, this would mean that daily foraging is occurring on pathways between sleeping sites. Thus sleeping trees could be of extreme importance in structuring the foraging and general forest use patterns (Anderson, 1998), and their study should be a high priority for future research on *C. m. ouakary*

The focus on predation

The apparent focus of *C. m. ouakary* on use of sleeping sites that maximize the possibility of avoiding nocturnal predators is rather curious since igapó does not appear to be a

predator-rich environment, at least in terms of such known primate predators as big cats (Gudger, 1946; Haugaasen & Peres, 2007b; Wallace *et al.*, 1998). Considered to be an opportunistic predator (Emmons, 1987), jaguar are unlikely to enter into flooded igapó when its main prey base (terrestrial medium-sized mammals: Seymour, 1989) is absent or at very low densities and the adjacent terra firme provides higher chance of hunting success. Mustelid predators such at tayra (*Eira barbara)* do occur in the igapó (Bezerra *et al.,* 2009), but they are too small to take any but the youngest uacaris. This would also be true of tree-hunting felids such as margays (*Felis weildii*: Emmons, 1987). However, given the efforts which adult primates will make to defend their offspring (Borries *et al.,* 1999; Broom *et al.,* 2004; Harris, 2007; Passamani, 1995; Shahuano Tello *et al.,* 2002), the possibility of predation by smaller nocturnal carnivores as a factor in structuring sleeping tree choice in uacaris (and other primates) should not be neglected.

Owls have been recorded as primate predators in the Palaeotropics (Hart, 2007; Isbell, 2005). Both of the two largest Neotropical owls (the crested owl, *Lophostrix cristata* and the great horned owl, *Bubo virginianus*) have populations which inhabit lowland rainforest. The latter is recorded as regularly taking prey exceeding 3kg (e.g. Zimmerman *et al*., 1996). Evidence for predation by owls on Neotropical primates appears sparse, with the only literature appearing to be Wright (1989), who notes that *B. virginianus* was a formidable predator of some populations of *Aotus*, and Rehg (2006) who lists *L. cristata* among the potential predators of his three study species of tamarin. *Lophostrix* has been recorded at Jaú (Borges, 2006; Borges *et al.*, 2001), and from its size (40cm) could be capable of taking a small (or juvenile) primate. *Lophostrix* is one of the world's least well-known owls (Barros & Cintra, 2009), and its feeding ecology appears to be completely

unknown. So, the possibility cannot be discounted that the threat of its predation may also contribute to the structuring of uacari sleeping tree choice.

Several authors, including Chapman (1988a,b: *Alouatta paliata, Ateles geoffroyi*), Di Bitetti *et al*. (2000: *Cebus apella*) and van Roosmalen (1985b: *Ateles paniscus*), have noted several animals sleeping simultaneously in the same tree, each on its own branch. The numbers involved are generally in direct relation to the size of the occupied crown. As shown in Section 4.3.6, this was not the case with the adult or near-adolescent golden-backed uacaris in the current study, which mostly slept alone. Where multiple animals were in the same canopy, with one exception out of 43 cases when five animals were grouped together, they were widely spaced within the canopy and occupied different branches. The significance of such solitary sleeping remains to be researched.

4.4.6 Communication

Vocalizations

Primate vocalizations comprise of two major forms of call: graded and discrete (e.g. Le Prell *et al.*, 2002). In *C. m. ouakary*, I observed that there seems to be a series of graded calls, the *twitter-trill-chok-cheng*, the first an indication of location, the second a combination of location-plus-discomfort, and the subsequent two indicating progressively higher levels of alarm. Other calls seem quite discrete and context specific. Interestingly, given the presence of separate alarm calls for different types of predator in other species of primate (e.g. Zuberbühler, 2000a,b for *Cercopithecus diana* and *C. campbelli*; Digweed *et al.*, 2005 for *Cebus capucinus*), the alarm call given for both jaguar and raptor were not obviously different to human listeners, though they have yet to be analysed acoustically.

A number of calls reported by other authors were not encountered by me when observing uacaris. These included weaning calls of juvenile uacaris (reported by Boubli,

1997a from two hand-reared juvenile *C. m. melanocephalus*), and the *Wee-ook* call from *C. c. ucayalii* which has not been recorded for either *C. m. melanocephalus* or *C. m. ouakary*. The graded nature of a *hic-chyook-chick* series parallel those reported for *bark-rhork-rhä* by Bowler (2007). The lack of parallels between the graded series of alarm calls for *C. m. ouakary* and *C. c. ucayalii* is unsurprising, since discrete and exact categorization is often very difficult for a human observer. Neither Boubli (1997a) nor Ayres (1986a) reported in any detail on the calls of their study animals.

Many primate species coordinate group movements with vocalizations (e.g. *Saimiri*, Boinski, 1996). There was no evidence in *C. m. ouakary* of the kind of long-call which, for example, *Ateles* use to maintain contact between dispersed sub-groups (Eisenberg, 1976; Ramos-Fernandez, 2008). Oppenheimer (1977) provided, for several Neotropical primates, extensive documentation of calls given by separate individuals seeking to be reunited with the rest of the group. Singleton uacaris were quite frequently encountered (Table IV-5), but almost never vocalized when travelling (in contrast, a band of uacaris, if not in flight, is a noisy affair). Even when feeding (a time when groups always uttered *twitter* calls), singleton uacaris remained silent. There appear to be no 'lost' calls such as are uttered by capuchins (Digweed *et al.*, 2007), sifakas (Fichtel, 2004) and others. Such calls have, however, been reported for *C. c. ucayalii* by Bowler (2007: as '*bark*' calls), being given by lone animals or animals in small groups and responded to with '*hic*' calls (probably equal to the '*twitter*' of *C. m. ouakary*) by the main body of animals. This may indicate both a prevalence of silence as a predator avoidance strategy and the relative commonness of foraging alone in the society of golden-backed uacari groups.

Van Roosmalen (1985b) reported that, proportionately, small groups of *A. p. paniscus* vocalized much less than large ones when travelling. Though I did not quantify it, this also appeared to be the case for *C. m. ouakary*. The significance of this is uncertain, though it may be a predator-avoidance strategy. Other aspects of *C. m. ouakary* social behaviour (aggression, play, and grooming) are discussed in Section 4.5.1.

Chemical communication

The use of scent as part of a species communication *milieu* is very common in lemurs and galagos, where it functions both to mark territory and inform on individual identify, social status and reproductive state (e.g. Watson *et. al* 1999; Lewis, 2006), and in Cercopithecines, where it is primarily associated with reproduction (Snowdon *et al*., 2006). In Neotropical species, scent-based communication is commonest in Callitrichids (Heymann, 2006), though it does also occur in larger species (e.g. Di Fiore *et al*., 2006: *Lagothrix lagotricha*; Hirano *et al*., 2008: *Alouatta guariba clamitans*).

I observed behaviour that could be interepreted as relating to chemical communication only three times in the 16-month of field observations. On one occasion, an adult female sitting on a branch used her legs to rachet her perianal area across the bark surface for some 30-40 cm. After she left, the area was quickly investigated by another band member of unknown sex. This individual was not seen to engage in flehmen, and was not sexable, an erect penis not being noted. A second (unsexed) individual engaged in ano-genital racheting behavior without eliciting any reponse from other band members. A third individual (an adult male) was seen to rub its chest on a horizontal branch on which it had been sitting. The behaviour involved the repition of the rubbing movement four times over a period of some 30 secs. No other band member was seen to investigate the spot on that or any subsequent day. No gouging behaviour was observed that might be associated with

deposit of compounds related to chemical communication (as occurs, for example, in *Propithecus* species: Patel & Girard-Buttoz, 2008, and marmoset species, Rylands, 1985). Ano-genital sniffing behaviours were not observed over the 16 months of field study. Nor were direct urine marking, anoiting of hands or feet with urine, or sniffing of branches during general movement.

This low level of chemical communication is what might be expected from a fast-moving, wide-ranging species with a social system sufficiently fluid that encounters between the same individuals may be infrequent (Zhang *et al*., 2009). Certainly, no other long-term study of the genus (e.g. Ayres, 1986; Boubli, 1996, Bowler, 2007, Bezerra, 2010) mentions behaviours associated with chemical communication, and such reports are also lacking from similar studies of the genus *Chiropotes* (e.g. Pinto, 2008). However, sternal glands have, been recorded in the genus *Cacajao* (Fontaine & DuMond, 1977 for *C. c. ucayalii*). It is not known if such glands are functional, but their presence clearly means that the possibility of occasional chemical communication in *Cacajao* should remain open. Certainly, olfactory communication does occur in *Pithecia* (e.g. Gleason, 1998). Here, however, territories and group sizes are small circumstances underwhich contact between particular individuals might be expected to be frequent, thus providing a more appropriate *milieu* for chemical communication.

4.4.7 Associations with Other Species

Species that travel with uacaris 1 – birds

As a review of literature (Hankerson *et al.*, 2006) has shown, associations between primates and other mammals, and primates and birds, have been reported for a wide array of primate taxa. These associations are often stable and may last for many days (Hankerson *et al*., 2006). In contrast, uacaris seem to associate very infrequently with

other species, be it bird or mammal. There appears to be no clear reason for this, though it is possible that the uacaris' very rapid rate of movement, and the general absence of the detailed searching for insects by uacaris, may explain the lack of association, since it may simply be hard for birds to integrate the time budget requirements of movement and effective foraging when trying to maintain proximity to a swiftly moving troop of uacaris. Rewards may, in any case, be small. It is notable that other species with which birds are commonly associated generally move more slowly and forage more for insects than uacaris (e.g. Boinski & Scott, 1988; Fontaine, 1980; Hankerson *et al.*, 2006; Heymann, 1992b for *Saimiri*, *Cebus*, *Leontopithecus* and *Saguinus*, respectively).

The absence of any observations of white hawks (*Leucopternis albicollis*: Accipitridae) following uacaris is a cause for surprise since these hawks are known to follow high canopy primates and feed on the arboreal snakes they disturb (Zhang & Wang, 2000), and *L. albicollis* is not uncommon at Jaú (Borges *et al.*, 2001). Those birds of the igapó which did appear to associate with uacaris, did so only for as long as the primates stayed in a particular area, and did not follow the primate group for many hours, as has been recorded with, for example, the double-toothed kites (*Harpagus bidentatus*: Accipitridae: e.g. Egler, 1991; Heymann, 1992b). This may be due to the fact that when moving, uacaris will leap to another branch to avoid passing through or leaping across any large colonies of epiphytes in their path.

Species that travel with uacaris 2 – aquatic species

For non-flooded forest primate species, it is common for them to be trailed by terrestrial frugivores who feed on the fruits they knock down or drop partly eaten. Mittermeier (1988), for example, states that acouchis (*Myoprocta*), agoutis (*Dasyprocta*), deer (*Mazama*), peccaries (*Tayassu*), as well as large birds such as curassows (*Crax*),

trumpeters (*Psophia*) and tortoises (*Geochelone*) were observed below fruiting trees occupied by *Ateles*. Similar associations have been observed in the aquatic realm below uacari feeding sites: Amazon pink river dolphins (*Inia g. geoffroyensis*: Iniidae) are reported to associate indirectly with uacaris, feeding on the fish that feed on the fruit that uacaris knock down (Defler, 2004). On eleven occasions, I observed fish (pacu, *Colossoma* sp., and matrinxã, *Brycon matrinchao* - both Characidae) feeding on uacari-deposited fruit in water beneath feeding trees. They also fed on many occasions on the primate's fæces. River turtles (*Podocnemis* and *Peltocephalus* spp. - both Podocnemididae) were also observed to bite floating fruits on which uacaris had fed, as well as feeding on a wide variety of fruits from lower-growing shrubs (Pérez-Emán & Paolillo, 1997; Teran *et al*., 1995). However, unlike the reports of Defler (2004), *Inia* were never observed feeding on the fish at these moments, though the dolphins themselves were regularly seen swimming in flooded igapó. The reasons for this are currently obscure.

Responses to potential predators 1 - birds

Primates use olfactory, visual and auditory cues to identify predators (e.g. Hayes & Snowdon, 1990; Suendermann *et al.*, 2008). They often show generalization to predator models, using key elements of predator appearance or behaviour to classify an animal as a potential danger (e.g. Coss *et al*., 2004; Emile & Barros, 2009; Ramakrishnan *et al.*, 2005), and also distinguish aerial and terrestrial predators (e.g. Gursky, 2007; Pereira & Macedonia, 1990; Seyfarth *et al*., 1980; Zuberbühler, 2000c, 2001).

An interesting form of generalization was reported for *Ateles p. paniscus* by van Roosmalen (1985b), where the monkeys became agitated, and gave low-level alarm calls when a flight response was observed in other diet species of their potential predators (including peccary, agoutis, curassow and trumpeters). This behaviour has not yet been

observed in any population of any species in the genus *Cacajao.* For *C. c. ucayalii*, Bowler (2007), observed incidences of alarm calls being falsely given to *Cathartes* and *Coragyps* vultures, but also reported uacaris would chase these birds from their perches. Boubli (1997a) also noted that *C. m. melanocephalus* gave alarm calls to overflying vultures (and also to toucans). In 945 hrs. of observation, Bowler (2007) saw one raptor attack: an unsuccessful attempt by a large eagle, either a *Harpia harpyja* or *Morphnus guianensis.* He also reports two incidents of tayra being mobbed by red uacaris uttering the same kind of *chick* calls with which unhabituated groups greeted ground-walking researchers.

From golden-backed uacaris' observed reactions to various avian species, it seems clear that they can discriminate which constitute a potential danger. Discrimination appears to include physical proximity of actual raptors, as well as a more generalized image of potential 'danger with wings'. This excludes both small birds, and some large ones, such as herons and egrets. Some ambiguity exists; vultures probably elicit a reaction because of their outline and flight pattern, green ibis and muscovy ducks probably because of their wing outline and dark colour. This form of generalization by *C. m. ouakary* concords with the way in which other primate species appear to learn what constitutes a danger in their environment (e.g. Coss *et al*., 2004; Griffin *et al*., 2001; Treves, 1999). Responses to raptor calls has been widely reported (e.g. Miller & Treves, 2007; Treves, 2002), as has the ability to distinguish between the calls of raptors and of other species of birds (e.g. Macedonia & Yount, 1991). Many Neotropical primates give alarm calls to raptor species, especially to harpy eagles (Robinson & Janson, 1987), a species capable of taking a full-grown howler monkey (e.g. Peres, 1990b).

Cacajao m. ouakary was observed dropping lower in the canopy when a raptor flew over or called nearby. This is a widely reported defensive response in primates (e.g. Karpanty & Grella, 2001 for lemurs and Treves, 2002 for review), and has been reported by Bowler (2007) for *C. c. ucayalii*, and by Vié *et al.* (2001) for *Pithecia pithecia*.

Responses to potential predators 2 – mammals

It is also clear that uacaris recognize the tayra as a potential predator and also know the call of a jaguar. These latter have been reported to take *Alouatta*, *Ateles* and *Brachyteles* (Matsuda & Izawa, 2008; Olmos, 1994; Peetz *et al*., 1992), and so uacaris would be within their size range, even if jaguar appear rarely to enter flooded igapó (pers. obs.). Successful tayra predation of a large primate has not been reported, though mantled howlers (*Alouatta palliata*) exhibit anti-predator behaviour in response to them (Asensio & Gómez-Marín, 2002), and Defler (1980) reported attempted tayra predation of a juvenile *Cebus albifrons* (on the other hand, Haugaasen & Peres, 2008 report *Saimiri* and *Eira* travelling together, albeit briefly, with no obvious agonistic interactions). Observed defensive reaction to the iguana by a juvenile uacari (reported in Appendix IV-2), may have been in mistake for a snake, as these have been reported predating the uacari sister genus *Chiropotes* (Ferrari *et al*., 2004). Though anacondas and boas are recorded from Jaú (Neckel-Oliveira & Gordo, 2004), and were observed by myself and other fieldteam members during the study, they were never observed in proximity to uacaris, so possible reactions are currently unknown. However, mobbing of snakes does occur in Neotropical primates (e.g. Bartecki & Heymann, 1987b), and several Cebid species possess specific mobbing calls (e.g. Izawa, 2002 for *Ateles belzebuth*).

Uacaris may give alarm calls for up to 20 minutes after a predation event by an eagle (Barnett *et al.*, in press: event in 2005). This kind of extended response to successful predators is common in primates (Treves, 1999).

Giant otters (*Pteroneura brasiliensis*: Mustelidae) are quite common at Jaú. I did not see uacaris and *P. brasiliensis* together. Bezerra *et al.* (in press) report that *C. m. ouakary* fled from giant otters, and posit that this is related to possible predation opportunities on those rare occasions when uacaris descend lianas or branches to drink from the surface of flowing waters (above). Though it would be very difficult to prove, the possibility should be considered that uacaris respond defensively to giant otters not because they might be potential predators *per se*, but because the uacaris mistake the otters for tayra, another mustelid, which is known to take (Bezerra *et al.*, 2009), or attempt to take (Defler, 1980), adult tamarins and the juveniles of larger primate species, and are considered as a threat by *Ateles p. paniscus* (van Roosmalen, 1985b), *Alouatta palliata* (Asensio & Gómez-Marín, 2002) and *Alouatta belzebul* (Camargo & Ferrari, 2007).

Primates are widely reported to respond to the alarm calls of other primate species (e.g. Fichtel, 2004), and of other animals (e.g. Zuberbühler, 2000a). However, I was not in the presence of a group of primates of another species on any occasion when uacaris gave alarm calls and so cannot say how such igapó-living forms as *Saimiri sciureus* and *Cebus albifrons* might have responded to them. Similarly, I never heard alarm calls of other primate species when watching uacaris, and so the nature of their response is similarly unknown. *Cacajao m. ouakary* certainly did not respond to contact calls of other igapó-living primates. Uacaris at Jaú appear rarely to associate with other primate species. This may make it difficult for them to observe and learn the contexts in which other species'

calls are given (Cheyney & Seyfarth, 2007; Flack & de Waal, 2007), as well as negating the need to respond to such calls in the complex and nuanced ways that have been recorded, for example, by Zuberbühler (2000b) for cross-species call responses by diana (*Cercopithecus diana*) and Campbell's (*C. campbelli*) guenons.

4.5 Cacajao melanocephalus ouakary in Context: comparing the current data with what we know from *C. calvus, C. m. melanocephalus* and *Chiropotes* spp.

Cacajao m. ouakary is a member of an evolutionary distinct lineage which, with its close congener *Chiropotes*, show anatomical, morphological and behavioural specializations for a diet dominated by hard-husked fruit the majority of which are patchily distributed in the high canopy. Aspects on diet will be examined in later chapters. Here I make comparisons between the new data on *C. m. ouakary* revealed by the current study and existing knowledge of the social ecology of *Chiropotes* and of other members of the genus *Cacajao.*

4.5.1 Social Behaviour: social structure, aggression levels, grooming and play

Social structure in the golden-backed uacari

When looking at groups of 4-6 uacaris, I never saw animals that could be identified as adult males together (though given the operational difficulties the significance of this is unclear). If these very preliminary observations actually reflect the true situation at Jaú, then they indicate a group structure that consists of '1 male: 1 female, with up to 3 attendant adolescents' (Knogge *et al.,* 2006), though it is possible that one of the adolescents might instead be a younger female. This structure could help explain the absence of observations of bachelor groups of golden-backed uacaris at Jaú (although such groups have been reported by Marcela Oliveira and Helder Quieroz for *C. m. ouakary* from Amanã, a site some 100km due south of Jaú: Barnett *et al.,* in press).

Bachelor groups are known for *C. c. calvus* (Ayres, 1986a), and in *C. calvus ucayalii* (Bowler, 2007), where they may number up to 10 adult and sub-adult males. In *Chiropotes satanus* adult males are affiliative, spending most of their time closest to other adult males (Veiga, 2006; Veiga & Silva, 2005). These are all taxa where fission-fusion sociality has been reported (Norconk, 2007).

As shown in Table IV-6, there is considerable variation in the number of *C. m. ouakary* which may be encountered travelling together. A similar level of flexibility has been recorded for *C. c. ucayalii* by Bowler (2007) who has pointed out that, to forage in such variably size of groups, uacari social organization must also be very flexible. Exactly how flexible it is in *C. m. ouakary* is currently unclear since the inability to identify individuals reliably during the current study has made it impossible to consider such aspects as the compositional continuity of the sub-groups, and whether long-term affiliations occur between the members of *C. m. ouakary* sub-groups. The consequences of the lack of substantial sustained inter-individual affiliations on aggression, grooming and play are explored below.

Whilst fission-fusion is known to occur in *C. m. ouakary* (Defler, 1999), as a species the golden-backed uacari appears to be associative but not gregarious; foraging groups are aggregations and not the call-coordinated socially-bonded bands that occur in *Ateles, Pan, Theropithecus* and other fission-fusion species.

Social behaviour: aggression levels, grooming and play

Aggression: One remarkable aspect of uacari society is the low level of aggression, with (other than boisterous play between juveniles) only four acts of physical aggression and one threat being recorded during the entire 101.8 hrs. of observation of uacaris (i.e. 0.049 events per hour). This low level of antagonistic interaction accords with the study of

black-backed uacaris by Boubli (1997a), who observed no aggressive interactions or threats for *C. m. melanocephalus* in 120.3 hrs. of observation across 16 months (though he observed one animal with recent scars that might have been the result of fighting).

The levels for *C. m. ouakary* and *C. m. melanocephalus* are in stark contrast with results of studies of other fission-fusion species such as members of the genus *Ateles.* Here regular male-male aggression has been observed, as well as lethal intra-group aggression (e.g. Valero *et al.,* 2006). To place figures from *C. m. ouakary* and *C. m. melanocephalus* in context, Miller (1996) reported that adult wedge-capped capuchins (*Cebus olivaceus*) experienced between 0.5 and 1 aggressive interaction per hour, and Hausfater (1975) reported 0.24 agonistic interactions per hour for savanna baboons.

It is currently unclear whether golden-backed uacaris are actually just not aggressive, or if observed low aggression levels are the results of the high levels of inter-individual spacing which simply lessen the rates of encounter between potential aggressors. However, Bowler (2007) has recorded near-daily incidences of aggression for the Peruvian red uacari on the Río Yavarí (mostly male-male, but also male-famale), and *C. c. ucayalii* density at this site is reported to be higher than anywhere else in the range of this taxon. Whilst this might be an influencing factor in the levels of aggression, Bowler (2007) reports not only that inter-individual distances are also often substantial, but that food is plentiful and so aggression-mediated resource competition (of the kind reported by Vogel *et al.,* 2007 for *Cebus capuchinus*) is unlikely. Also, aggression occurred across all study months and did not appear to correlate with variations in levels of resource abundance (Mark Bowler, pers. comm.), nor with the mating season.

This difference between *C. c. ucayalii* and *C. m. ouakary* in levels of aggression might be explainable if sub-groups in *C. m. ouakary* showed little or no affiliation, while those of *C. c. ucayalii* did associate together more often than random. This would provide *C. c. ucayalii* with more frequent opportunities for individual recognition and interactions – key elements in the formation of a social structure (e.g. Ghazanfar & Santos, 2004). The differences in levels of aggression correlate with the markedly dissimilar levels of dimorphism in physical appearance and tooth size between the two taxa. Males of *C. m. ouakary*, whilst some 6.4% larger than females (Hershkovitz, 1987a), very strongly resemble them in shape and colour. On museum skulls their teeth are the same in proportion (Hershkovitz, 1987a). This is not the case with *C. c. ucayalii* where males, though only 4% larger (Hershkovitz, 1987a), have proportionately larger jaw than females (Bowler, 2007), as well as larger canine teeth. The increased volumes of associated jaw musculature result in the adult males' highly characteristic appearance (Fig. IV-5). In addition, the enlarged canines of males (but not females) appear to be used in aggressive displays, both to human observers, and to each other (Fontaine, 1981). No comparable behaviours were observed for *C. m. ouakary* during the course of the current study. *Cacajao m. melanocephalus* also has very low levels of recorded aggression (Boubli, 1997a, 1999), and, like *C. m. ouakary*, male *C. m. melanocephalus* do not develop hypertrophied *temporalis* muscles on becoming adult (Barnett, 2005; Hershkovitz, 1987).

Adult female

Adult Male (Photos: Mark Bowler)

Fig. IV-5: **Cacajao calvus ucayalii*, Showing Male's Larger* Temporalis *Muscles***

The breeding system of *C. m. ouakary* cannot be elucidated from current field observations. Hershkovitz (1993) used penile morphology to predict a multi-male sperm competition based system. Dixson (1998), based on the pattern of intromissions and pelvic trusts derived from Fontaine's (1981) studies of semi-captive *C. c. ucayalii*, considered *Cacajao* to possess a multimale-multifemale system. However, from Kay *et al*. (1988)'s model linking dental dimorphism with breeding system, it might be predicted that *C. m. ouakary*, with low canine dimorphism will have a polyandrous or monogamous social structure. The high levels of male aggression and high levels of canine dimorphism (compared to *C. m. ouakary* and *C. m. melanocephalus*) recorded for *C. c. ucayalii* by Bowler (2007) are in accordance with Kay *et al*.'s model.

Such a model would predict greater levels of male-male tolerance in *C. m. ouakary* than in *C. calvus*, and this might be reflected in differences in inter-individual distances in the former species. This contention cannot currently be proven with available data since,

whilst Bowler (2007) provides extensive documentation on the proximities of various combinations of age-sex classes, he does not record actual nearest neighbour distances. However, it is worth noting that *Brachyteles* also display very low aggression levels (0.025/hr, Strier, 1992), have little canine dimorphism, multi-male societies and genitalia indicative of sperm-competition. It is possible that in Neotropical primates there exist two forms of fission-fusion society: the aggressive *Ateles* model and the peaceful *Brachyteles* form and that, for reasons as yet undiscovered, the *calvus* clade of uacaris has followed the former, while the *ouakary-melanocephalus* clade pursued the latter.

Grooming

Proximity and grooming are two major affiliative behaviours in primates (e.g. Cheyney & Seyfarth, 1992: *Cercopithecus*; Cheyney & Seyfarth, 2007: *Papio*; Chiarello, 1995: *Alouatta*; Der Waal, 2000; *Pan*; Ventura *et al*., 2006: *Macaca,* and Schino & Aurelli, 2008 for review), with posited social functions ranging from access to food (Frank, 2008; Fruteau *et al*., 2009), affirmations of kinship (Nikitopoulos & Cords, 2008), affirmation of social bonds (Schino, 2007), agonistic support against male aggression (Schino *et al*., 2009), demonstration of relative positions in social hierarchy (Ventura *et al*., 2006), exchange for access to infant handling rights (Fruteau *et al*., 2009; Gumert, 2007), maintaining hygiene of skin and hair (Hill & Nash, 2007; Tanaka, 1995), reduction of aggression (Schino *et al*., 2005), to reduction of tension and distress (Aureli & Yates, 2010; Wittig *et al*., 2008). In primates, grooming is of sufficient social importance for there to be a specific series of associated postural, facial and vocal behaviours (e.g. Brockett *et al.,* 2000 for black howler, *Alouatta pigra*; Hoolahan & Strum, 2008 for *Papio* spp.; Oki & Maeda, 1973 for *Macaca fuscata*; Skinner, 1986 for Geoffroy's tamarin, *Saguinus geoffroyi*; Spinelli *et al*., 2009 for vervets, *Chlorocebus pygerythrus*). In line

with this variety of social functions, grooming may occupy significant portions of the day for many primate species: 10% for widow titi, *Callicebus torquatus* (Kinzey & Wright, 1982); 5% for grey-cheeked mangabys, *Lophocebus albigena* (Chancellor & Isbell, 2008), 4.9-8.2% for *Macaca fuscata* (Tsukahara, 1990); 8.38-17.79% for *Pan troglodytes* (Kosheleff & Anderson, 2009); 7% for white-faced saki, *Pithecia pithecia* (Vié *et al*., 2001); 7.6% for François langur, *Trachypithecus françoisi* (Huang *et al*., 2007).

Even though is not a major component for all species (e.g. grooming comprised just 1.53% of the time budget of a group of Geoffroy's black-and-white colobus, *Colobus vellerosus,* studied by Teichroeb *et al.,* 2003), the near-absence of social grooming from the time-budget of *C. m. ouakary* in the current study clearly requires some explanation, especially since this behaviour is also present only at very low levels in other members of the genus (e.g. *C. c. ucayalii*, 1.8%; Bowler, 2007). For *C. m. melanocephalus,* Boubli (1997a) observed grooming on nine occasions in a 16-month study. In five cases these involved an adult female and a juvenile, approximately 2 years old. Bouts lasted for up to 20 mins. The four others involved pairs of adults, once an adult male and female.

Three possible explanations present themselves for the lack of grooming in the uacaris: 1, uacari social ecology, 2, uacari activity budgets, and 3, lack of ectoparasites.

Social ecology and the absence of grooming: Social grooming was observed only 12 times during the current study, each time only between adolescents. In *C. c. ucayalii*, Bowler (2007) observed all age-sex classes allogrooming except sub-adult males. The possibility of some fundamental aspects of uacari social ecology being responsible for the observed lack of grooming rest on the following series of observations – i) several authors have noted the importance of grooming as a promoter of affiliative bonding against male acts of

aggression (e.g. Cheyney & Seyfarth, 2007 for *Papio*; Matsumoto-Oda & Oda, 1998 for *Pan*; Perry, 1997 for *Cebus*), yet both *C. m. ouakary* and *C. m. melanocephalus* notably lack reports of aggressive interactions; ii) kinship affirmation among females and the affirmation of matrilines are important functions of grooming (e.g. Cheney & Seyfarth, 2007 for *Papio*), yet in the highly fluid fission-fusion system that uacaris appear to possess the possibility exists that no inter-group kinship exists beyond the mother-most-recent-offspring and possibly the two most recent preceeding sibs. This lack of structured matrilines would be especially likely if *Cacajao* followed the model of other fission-fusion species, such as *Ateles, Brachyteles, Cebus, Chiropotes*, *Eulemur*, and *Pan* and the female was the disperser sex (Symington, 1987b; Coles *et al*., 2008, Izar & Nakai, 2006; Veiga *et al*., 2006; Toborowsky, 2008; and Anderson *et al.*, 2002, respectively). Certainly, the presence of male-affiliative behaviour and the presence of bachelor groups in both *C. c. ucayalii* (Bowler, 2007; M. Bowler, pers. com.) and *Cacajao*'s close taxonomic relative *Chiropotes* (Veiga & Silva, 2005), point towards this possibility; iii) the large physical distances between foraging parties might play a role in the lack of grooming, especially because of the density of vegetation in which uacaris generally forage. Because of this, even if related females existed within the larger body of uacaris moving in the same general direction at the same time, such individuals might be so separated that visual and auditory communication would not be possible. Hence knowledge of how other union members responded to various social events (e.g. Cheyney & Seyfarth, 2007) would not be available and regular social updates required for an affiliative union based on reciprocity could not be conveyed. How uacaris forage, rest and sleep may also be influential. I never observed more than five individuals foraging simultaneously in the

same tree (Table IV-11), and even then only in such large ones that individuals were widely spaced in an extensive canopy. This limits the opportunities for social bonding through affiliative co-feeding, an act where any tension is often mitigated through grooming bouts (e.g. Ventura *et al*., 2006). In addition, I did not see more than five individuals sleeping in the same tree (Section 4.3.6). This also limits the opportunities for grooming and associated affiliative interactions. iv) grooming so often occurs during resting that many primate time budgets conflate the two (e.g. Huang *et al.,* 2007 for *Trachypithecus francoisi*; Nakagawa, 1989 for *Erythrocebus patas*; Yang *et al*., 2007 for *Trachypithecus francoisi*). Uacaris were never observed to rest with more than three animals to a tree (section 4.3.4, 4.3.7). It appeared that these were always the same animals which had been travelling and foraging together. Resting trees seemed widely separated. These features also limit opportunities for wide-spread social interaction during daily rests.

Thus, as a species, *C. m. ouakary* appears to be associative but not gregarious and foraging groups are call-coordinated aggregations not socially-bonded bands as occurs in *Ateles, Pan, Theropithecus* and other fission-fusion species (e.g. Ramos-Fernández, 2005, 2008). With aggression reduced by the tendency to forage in a widely-seperated mannar, the resulting loose social structuring may mean that grooming compatriots may simply not be important. As Lehmann *et al.* (2007) have pointed out, in very large groups, or those where fission-fusion is frequent, group cohesion may be too low for grooming to function in its familiar role as social glue of primate societies. Fieldwork on *Papio cynocephalus* (Henzi *et al*., 1997) supported Dunbar's (1991, 1993) contention that there exists a certain minimum level of social interaction below which female networks weaken and grooming-based affiliative behavior ceases to function as a social medium. Whilst this appears to be

facultative in *Papio* baboons (e.g. Galat-Luong *et al.*, 2006; Henzi *et al.*, 1997; Henzi & Barrett, 2005), it may well be obligate in uacaris.

For *C. calvus*, it is possible that grooming acts, as it does in many potentially aggressive species, as a pacifier between individuals, mollifying potentially dangerous or lethal interactions (Dunbar, 1991). Higher grooming levels are also known from other more aggressive species of Neotropical primate with fission-fusion, such as those in the genera *Ateles* and *Lagothrix* (Fedigan & Baxter, 1984; Stevenson *et al*., 1998a, respectively).

Time budgets and the absence of grooming: Grooming, and being groomed, takes time: Perry (1996) found an individual female *Cebus capuchinus* to be groomed on average for 22.4 secs every waking hour over a two month period, while Manson *et al.* (1999) reported averages of 80 secs/ hr for individuals of the same social group, while in 126.9 observation hrs., Sánchez-Villagra *et al*. (1998) recorded 118 allogrooming events in *Alouatta seniculus*, each lasting an average of 109 secs. In primate time budgets the apportioning of time between various aspects of behaviour (such as foraging, resting or social behaviours), appears to be highly constrained (Hill, 2003: *Papio cynocephalus*; Hill & Dunbar, 2004 for the genus *Papio*). Time constraints have been shown to be important in determining not only who receives grooming, but the amount of overall time that a grooming individual invests in this activity (Berman & Kapsalis, 2009: *Macaca mulatta*; Berman *et al.*, 2008: *Macaca thibetana*). Thus, given the large proportions of the time budget devoted to moving and foraging in uacaris (tables IV-3 and IV-4), it may be that uacaris simply do not have the time to invest in socially-affiliative grooming, especially if those in whose company they spend the rest hours when potential grooming occurs are those with whom they have already spent the entire day. When larger associations do

occur, they involve moving, not feeding or resting and so opportunities for grooming or any other affiliative behaviour (such as increased proximity or co-feeding: e.g. Ventura *et al.,* 2006) are strictly limited.

Ramsey & Beram (2007) note that both playing and grooming are conflict management strategies in the Celebes crested macaque (*Macaca nigra*). It is possible that these resolutive behaviours are not required in *C. m. ouakary* society as the near-absence of social interaction means there is little social stress. The lack of social interactions may simply be the twin results of the individuals being members of a loosely affiliated group of highly time limited individuals who need to move far and fast on a daily basis to meet quotidian energy requirements.

In this context, it is notable that for smaller Pitheciines such *Callicebus torquatus,* in which live in small groups based around monogamous adult pairs, and have short daily travel distances, grooming represents between 2.7% (Easley, 1982) and 10% (Kinzey & Wright, 1982) of the time budget, while in the larger (but also monogamously paired) *P. pithecia,* an adult pair may spend up to 7% of their time grooming.

Time budgets and the absence of ectoparasites: Primate fur may conceal a considerable ectoparasite load (e.g. Sánchez-Villagra *et al*., 1998), and though grooming does have strong functions in social bonding (Schino, 2007; Ventura *et al*., 2006) and stress reduction (Wittig *et al.*, 2008), studies have also revealed that it does also have the utilitarian function of cleaning the pelage and skin and removing ectoparasites (Dunbar, 1991; Hutchins & Barash, 1976; Tanaka, 1995). Ticks, lice and fleas are the main primate ectoparasites (Hutchins & Barash, 1976), but botflies, fur mites (Troyo *et al*., 2009) and leeches (Wright *et al*., 2009) may also be present. Studies with a pet *Cercopithecus* by

Freeland (1981) indicated that the potential to gain ticks is great, yet wild-shot animals rarely had any (Garnham, 1957). However, body areas with longer hair are both more infested and more groomed (Freeland, 1981), and, though there is considerable inter-species variability in infestation levels, species with longer body hair generally have a higher ectoparasite load (e.g. Junge, 2006). Uacari body hair is notably long (Chapter 1), but, in the absence of any published studies of the ecoparasites of *Cacajao* it is not possible to take this line of enquiry any further. However, it is interesting to note the many records of self-medication by primates, some of which are against ectoparasites (Huffman, 1997). As many of the seeds eaten by *C. m. ouakary* are rich in secondary compounds (Schultes & Raffauf, 1990), it is possible that such compounds may enter the blood and deter or kill haematophageous species.

Play

In the current study, play was observed neither between adults, nor between adults and juveniles. However, extensive play was observed between adolescents. In one small study group this also involved the single most recently born individual, as soon as this individual was large and coordinated enough to participate. Play appeared to occur only when the adults were paused and feeding, or foraging and moving slowly. When the group was actively moving between feeding localities, the adolescents kept pace with the adults and did not play. Both Bowler (2007) and Boubli (1997a) observed very low levels of play, though Fontaine (1981) reported that, in semi-captivity, adult *C. c ucayalii* frequently interacted in a playful manner with juveniles.

4.6 Summary

In terms of comparisons with other Pitheciines, the most significant observations on the behaviour of the golden-backed uacari from the proceeding sections are:

- the low levels of social aggression (Section 4.5.1)
- the low levels of grooming and general lack of proximity (Section 4.5.1)
- the apparent presence of two peaks of reproduction (Section 4.5.1)

The key observations of this chapter were:

- Golden-backed uacaris spend an annual average of 32.9% paused feeding, 9.9% moving feeding, 48.1% moving travel, 5.1% rest, 4% social behaviour
- Group spread is often extensive
- Most activity takes place in the upper canopy and in emergents
- Sleeping trees are either used once or reused very infrequently. Nature of chosen trees indicates they are primarily chosen for their anti-predator properties
- A vocal repertoire of 11 calls was registered, some graded call series appear to express intensities, others warn of threats from perceived potential predators
- Uacaris appear to be able to distinguish predatory and non-predatory mammals and birds, and estimate predator distance and likelihood of threat

CHAPTER 5

DIET AND FEEDING BEHAVIOUR

Feeding is such a universal and commonplace business that we are inclined to forget its importance. The primary driving force of all animals is the necessity of finding the right type of food and enough of it.

Charles Elton, 1927

5.1 Introduction

It is rare for any heterotrophic organism to eat available foods in direct proportion to their availability. For non-sessile organisms, like primates, diet item choices reflect a trade-off between distribution, availability and digestibility (Ianson & Villalba, 2006; Oates, 1987). The temporal and spatial patterns of distribution and the net energetic yield of diet items, once the cost of obtaining, processing, detoxifying and digesting them is subtracted from their gross energetic yield, are all factors which impinge on the social and reproductive ecology of primates (Fashing *et al.*, 2007; Ganas *et al*., 2009; Jildmalum *et al*., 2009;Yamashita, 2008).

The majority of primate diets contain varying proportions of fruit, insects and leaves (Milton, 1984). Pitheciines are not the only primates to use immature fruits extensively (e.g. Baboons: Kunz & Linsenmeier, 2008a,b; Colobines: Wasserman & Chapman, 2003; Orangs: Ungar, 1995; Sifakas: Hemingway, 1996), but they are unique among primates in that immature fruits, and especially their seeds, dominate the diet (Kinzey, 1994). In such fruits, developing seeds are often protected either by secondary (often toxic) compounds (Freeland & Janzen, 1974; Lucas *et al*., 2001), or by physical defences that often result in the outer husk being a combination of thick, hard, and latex rich (Kinzey & Norconk, 1990; Lucas *et al*., 2001). Resolving the resultant challenges has required a unique set of anatomical, morphological, physiological and behavioral specializations,

whose interactions with the environment have already been explored extensively for members of the pitheciine genera *Pithecia* (e.g. Cunningham & Janson, 2006, 2007; Gleason & Norconk, 2002; Harrison-Levine, 2003; Norconk, 2006; Palminteri *et al*., 2005), and *Chiropotes* (e.g. Boyle *et al.*, 2009; Pinto, 2008; Port-Carvalho & Ferrari, 2004; Silva & Ferrari, 2009; Veiga, 2006), and which are now beginning to be investigated for *Cacajao* (Ayres, 1986a; Boubli, 1997a; Bowler, 2007; Bowler & Bodmer, 2009).

Until the current study, no long-term investigation of the *C. m. ouakary* diet had been conducted. All that was known came from the work of Defler (2004) on *C. m. ouakary* in Colombia, and short studies in Brazil in the Cabeça de Cachorro region of north-west Brazilian Amazonia (Barnett & da Cunha, 1991; da Cunha & Barnett, 1990), and in central Brazilian Amazonia (Barnett *et al*., 2005). These data were summarized in Barnett (2005). More recently, a series of studies of *C. m. ouakary* by Marcela Oliviera and Helder Quieroz in the Amanã Sustainable Reserve (Barnett *et al*., in press) have provided additional dietary information.

Previous published studies of *C. m. ouakary* were of short duration and not accompanied by quantified phenological data. Though all reported unripe seeds in the diet, the studies were not systematic and only a small number of items were registered. For example, a short study on the Curicuriari and Uaupes rivers (Barnett & da Cunha, 1990; da Cunha & Barnett, 1990), registered three diet items. Several short studies at Jaú, lower Rio Negro, between 1999 and 2005 (Barnett *et al.*, 2002; Barnett *et al*., 2005a,b,c), registered a total of 20 diet items, while Oliveira and Queiroz noted 24 species being eaten by golden-backed uacaris at the Amanã Sustainable Development Reserve,

Brazilian Amazonia (Barnett *et al.*, in press), of which they identified 13 taxonomically. At Caparú, Colombian Amazonia, Defler (2004) recorded *C. m. ouakary* eating 20 diet items. The data were not quantified in terms of feeding bouts or time budgets, and neither were the physical nature of fruits and the respective abundances of the food trees quantified in ways that might help explain any observed preferences for particular types of foods, or for the particular species involved. Yet such data are fundamental if any future conservation planning is to be effective, as they allow key features of the habitat to be understood and prime areas to be sought and, where possible, conservation programes initiated. In consequence, the current chapter seeks to provide the first long-term detailed description of the diet of the golden-backed uacari, how it varies over the course of an annual cycle of resource availability, and possible factors influencing diet choice. The conservation implications are considered in Chapter 7.

5.2 Aims

Because our knowledge of the diet of the golden-backed uacari is at such an initial state, the main aims of this chapter were to find out:

- What does *C. m. ouakary* eat at Jaú?
- When does it eat these things?
- Why does it eat them?

These primary aims were met by a study structured with the aims to:

- establish diet constituents of *C. m. ouakary* across the seasons, and record how monthly diet composition reflected potential food item availability
- quantify physical aspects of food items and compare with non-food items

- calculate Selectivity Indices for eaten items and investigate what influences diet item selection
- observe how uacaris obtain food, including fine details of food processing
- investigate incidence of predation on free-ranging arthropods and those inside fruits
- assess diet characteristics using fæcal analysis.

5.3 Results

5.3.1 Diet Composition

Plant diet of uacaris at Jaú

I obtained 11,902 records of golden-backed uacaris feeding on plant materials. Of these, 2452 (20.6%) were made in Phase 1, a total of 7765 (65.2%) in Phase 2 and 1685 (14.2%) in Phase 3.

For the plant-based part of the diet, a total of 189 diet items from 17 categories was recorded across 136 identified taxa in 87 genera from 44 families (Appendix V-1). Additionally, 12 plant taxa remained unidentified even to family, making a total of 148 taxa registered in the diet of *C. m. ouakary* at Jaú. Of the identified plant taxa, 40 (29.4%) came from terra firme, and the remaining 95 (70.6%) from igapó. No diet species were common to both habitats, though nine genera and eight families were shared. For both habitats combined, the top five families, in terms of number of feeding records were Sapotaceae, Lecythidaceae, Fabaceae, Combretaceae and Euphorbiaceae (Fig.V-2). Overall, the most speciose families in the diet of *C. m. ouakary* were Fabaceae (19 species), Sapotaceae (19 species), Lecythidaceae (10 species), Myrtaceae (9 species), and Euphorbiaceae (8 species). Of the 136***** identified plant taxa in the diet, five (3.6%) were bushes, 36 (26.3%) were understory trees, 70 (51.1%) were canopy trees, three were

palms (2.2%), five (3.6%) were epiphytes, and 18 (13.2%) were lianas. (***Note***: one species, *Simaba orinocensis* [Simaroubaceae], was encountered as both a tree and a liana, and was therefore counted in both categories and N=137 was therefore used for these percentage calculations). The commonest category of identified diet plants was 'canopy trees in igapó' (49 species, 35.8% of 137 records).

Thirty-three families had 10 or more feeding records, and ten families had nine or fewer. Ninety-two feeding records were from unidentified plants. Family totals for feeding records appear as part of Appendix V-1. The ten families with the greatest number of feeding records (range 147-3829) contributed 91.5% of these data (10,899 of 11,902 records). Their proportional contributions to the whole plant-based diet are shown in Fig. V-1.

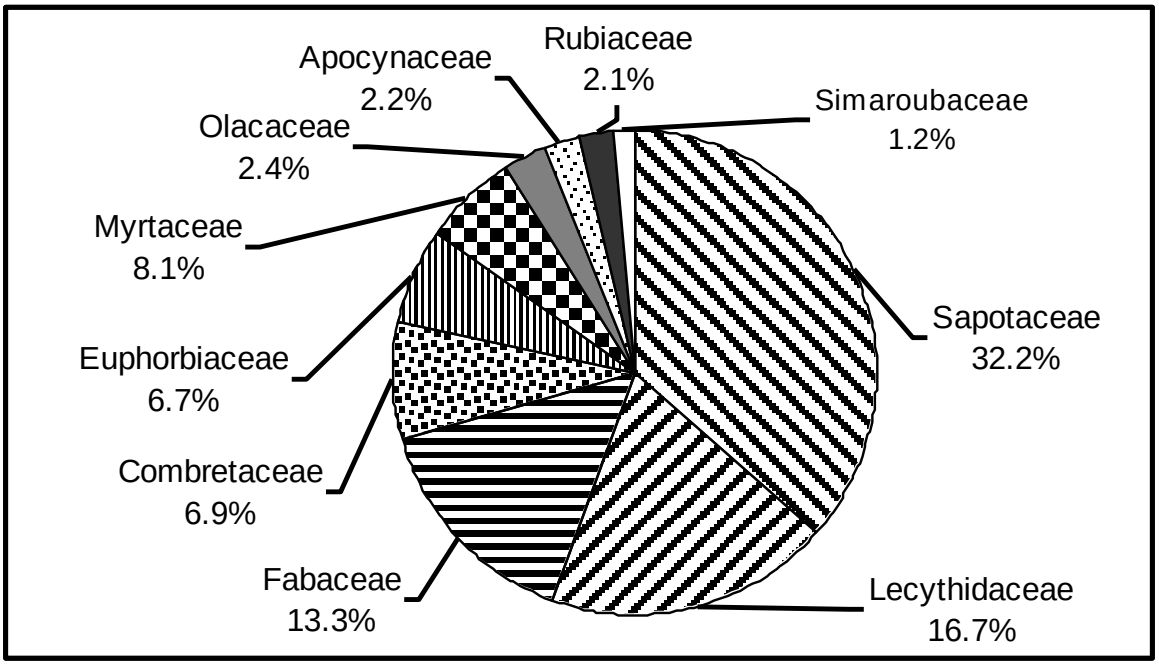


Fig. V-1: Plant Families Ranked 1-10 by Feeding Records in Uacari Diet

Of the 189 plant diet items, 95 (50.2%) were immature seeds; 35 (18.5%) leaves and leaf buds; 22 (11.6%) arils, pulp and small whole fruit; 20 (10.6%) flowers and flower

buds; 9 (4.8%) mature and germinating seeds; and 8 (4.2%) other parts (pith, pseudobulbs). Of 8719 diet items eaten for their seeds, 79.9% (N=6974) of the feeding records of this category were for immature seeds, while arils, pulp, germinating seeds and small whole fruit constituted remaining 20.1% (N=1745). These data are shown in Fig. V-2. In addition, there were two observed instances of mycophagy (<0.1%).

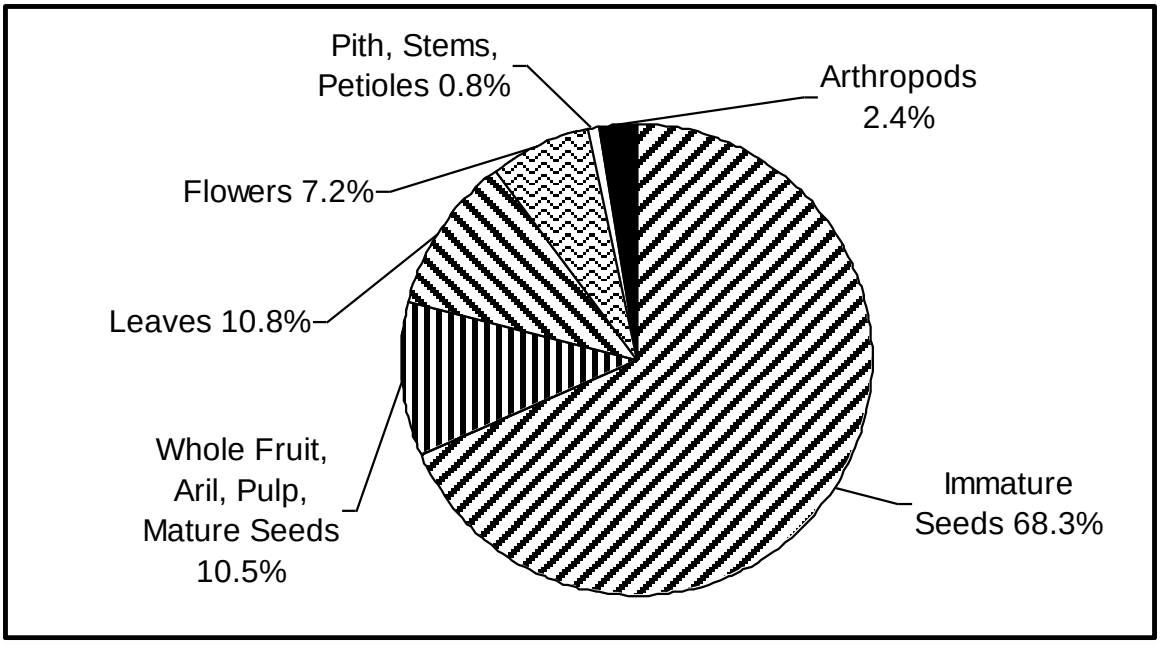


Fig. V-2: Annual Diet of Golden-backed Uacari

Eleven species were eaten in all three Phases of resource availability (*Aechmea mertensii, Aldina heterophylla, Codonanthe crassifolia, Eschweilera tenuifolia, Hevea spruceana, Hydrochorea marginata, Mabea nitida, Macrolobium acaciifolium, Pouteria 'cabecudo'* 1, *Pouteria elegans*, *Swartzia acuminata*), In addition, 20 plant species (14.7% of 136 identified taxa) were eaten for more than one anatomical part (e.g. both flowers and young leaves: appendices V-1 and V-2).

Table V-1, 2 and 3 give the top ten species eaten by habitat and by Phase. Appendix V-1 includes the rank value for each species when all identified taxa are ordered by number of total feeding records.

Table V-1: Top Ten Eaten Diet Items for Igapó and Terra Firme for* Cacajao melanocephalus ouakary *at Jaú National Park, Brazil: Phase 1

Terra Firme			***Igapó***		
Species	***Part***	***No. Feeding Records***	***Species***	***Part***	***No. Feeding Records***
Pouteria gomphifolia	immature seeds	278	*Eschweilera tenuifolia*	flowers	225
Lecythis pisonis	young leaves	55	*Micropholis venulosa*	immature seeds	176
Chrysophyllum s. sanguinolentum	immature seeds	52	*Mabea nitida*	immature seeds	169
Inga obidensis	aril	49	*Eschweilera tenuifolia*	germinating seedlings	168
Eschweilera wachenheimii	immature seeds	43	*Eschweilera tenuifolia*	immature seeds	121
Tocoa sp.	immature seeds	38	*Buchenavia ochrogramma*	immature seeds	103
Bombacopsis macrocalyx	immature seeds	32	*Swartzia acuminata*	whole immature fruit	87
Salacea sp.	immature seeds	15	*Pouteria elegans*	immature seeds	83
Chrysophyllum sparsifolium	immature seeds	9	*Hydrochorea marginata*	young leaves	69
Astrocaryum jauari	whole immature fruit	8	*Buchenavia* sp.	young leaves	58

Table V-2: The Top Ten Eaten Diet Items for Igapó for* Cacajao melanocephalus ouakary *at Jaú National Park, Brazil: Phase 2

Igapó: Phase 2		
Species	***Part Eaten***	***No. Feeding Records***
Micropholis venulosa	immature seed	1612
Eschweilera tenuifolia	immature seed	642
Buchenavia ochrogramma	immature seed	511
Pouteria elegans	immature seed	434
Chaunochiton lauranthoides	immature seed	277
Chromolucuma rubiflora	immature seed	277
Eschweilera tenuifolia	mature flower	209
Eugenia gomesiana	immature seed	202
Pouteria 'cabeçudo' 2	immature seed	190
Mabea nitida	immature seed	178

In Phase 2 there were also two terra firme feeding records, both for mature *Ficus* leaves.

Table V-3: The Top Ten Diet Items Eaten in Igapó for* Cacajao melanocephalus ouakary *at Jaú National Park, Brazil: Phase 3

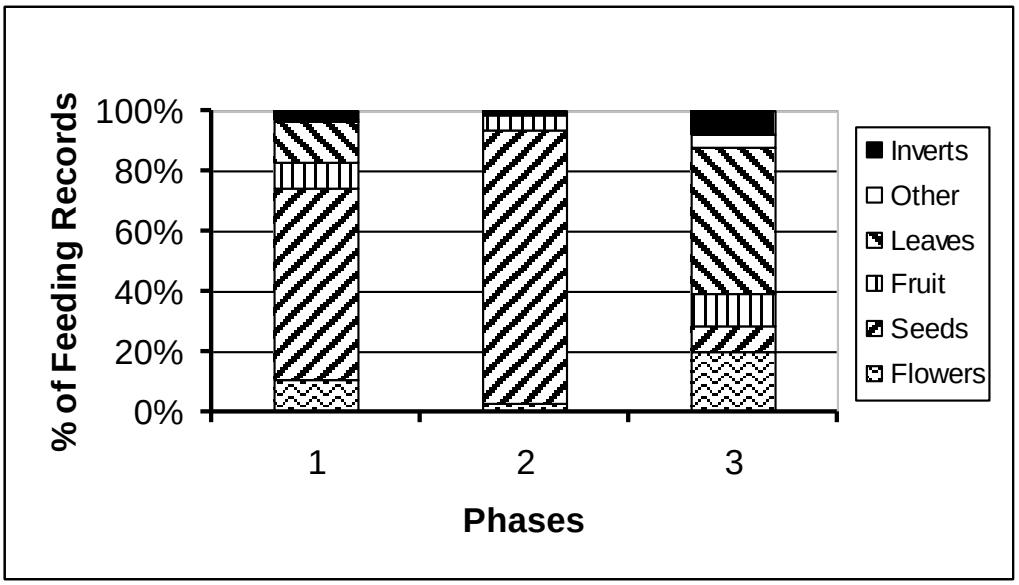
Igapó: Phase 3		
Species	**Part Eaten**	***No. Feeding Records***
Couratari c.f. *tenuicarpa*	mature flower	187
Hydrochorea marginata	young leaf	152
Swartzia acuminata	young leaf	127
Ormosia sp.	young leaf	113
Buchenavia ochrogramma	young leaf	111
Tontalea sp.	pulp	88
Aldina heterophylla	immature seed	55
Macrolobium acaciifolium	young leaf	52
Mouriri guianensis	immature seed	43
Hevea spruceana	young leaf	42

There are no terra firme records from this phase.

Ranked by number of feeding records per species, the combined feeding records of the top ten plant species of the three phases from both habitats comprised 61.7% of all feeding records (N=7342). Of the 30 species represented, seven species occurred in more than one phase, or had more than one item frequently eaten. Fifteen species were eaten for their immature seeds, and eight for their young leaves. When all feeding records for all feeding partas are combined, the top ten of all (*Micropholis venulatus,* 1788; *Eschweilera tenuifolia,* 1676; *Buchenavia ochrogramma*, 742; *Pouteria elegans*, 565; *Swartzia acuminata*, 484; *Mabea nitida,* 397; *Hydrochorea marginata,* 285; *Pouteria gomphifolia¸* 278; *Chaunochiton loranthoides*, 227; *Chromolucuma rubiflora*, 227) comprised 58.9% (N=6769) of all feeding records.

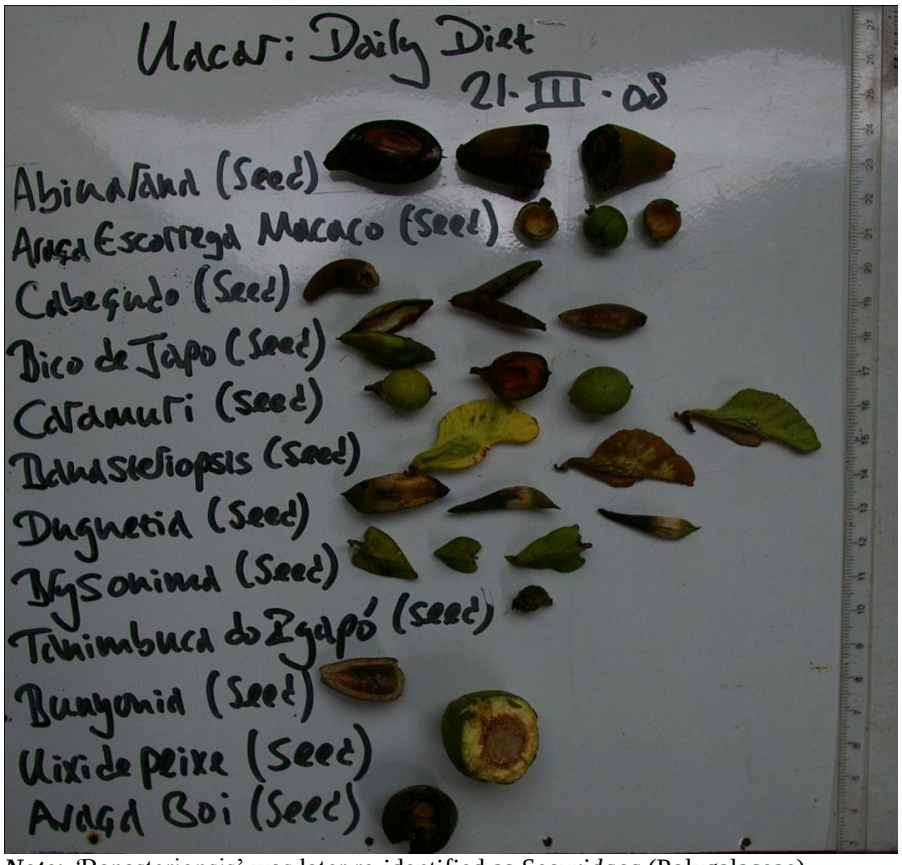
Seasonal differences in diet

Proportions of diet categories: As shown in Fig. V-3 there was considerable temporal variation in the proportions of diet categories used in the three phases of resource availability, with the diet in Phases 1 and 2 being dominated by immature seeds and in Phase 3 by young leaves and flowers. Fig. V-4 shows a sample of a daily diet.



Note: 'Seeds' = immature seeds only. 'Fruits' includes pulp, and whole fruit (including mature seeds).

Fig. V-3: Variation in Proportion of Food Types across Phases



Note: 'Banasteriopsis' was later re-identified as *Securidaca* (Polygalaceae)

Fig. V-4: **Cacajao melanocephalus ouakary** ***Daily Diet, Illustrating Diversity of Form and Species***

Animals in the diet of uacaris at Jaú

In addition to the 11,902 feeding records of plant-based items, I recorded a further 297 feeding records consisting of predation on animals. These consisted of 26 invertebrate taxa in at least eleven families and nine different orders (Appendix V-3). Of these, 98 feeding records (33%) were in Phase 1, 55 (18.5%) in Phase 2 and 144 (48.5%) in Phase 3. No records of predation on vertebrates were recorded.

Seasonal changes in diet breadth of uacaris at Jaú

Figs V-2 and V-3 show the proportions of all 12,199 combined animal and plant feeding records represented by simplified plant diet item categories (5.2.2 provides definitions for all 17 original categories whence these were derived), and for arthropods. Extending this, Table V-4 provides a summary of diet breadth (in terms of number of species exploited) per habitat and Phase. The background data, summarizing the number of species eaten per diet category, in igapó and terra firme for all three phases, is given in Appendix V-4.

Table V-4: Diet Diversity and Number of Species Eaten by* C. m. ouakary *in each Phase and Habitat

Habitat & Phase	*Total Plant Diet Items*	*Total Animal Total Spp.*	*Total No. Diet Items*
Phase 1 - Ig	41	10	51
Phase 1 - Tf	38	2	40
Phase 2 - Ig	67	13	80
Phase 2 - Tf	1	0	1
Phase 3 - Ig	79	12	91
Phase 3 - Tf	3	0	3

The highest number of plant items eaten was recorded in igapó during Phase 2, a high proportion of items in the diet in this Phase (68%) were from a single diet item class, immature seeds. The number of recorded items is consistently higher in igapó than terra firme. Overall, the number of diet items (animal and plant combined) is greatest in Phase

3 igapó (N=91). This is the part of the annual cycle at Jaú where there is the lowest availability of fruits and seeds. The total number of diet items recorded in Phase 3 igapó is 113.8% higher than Phase 2 igapó, 178.4% higher than the number recorded in Phase 1 igapó, 227.5% higher than the number of diet items in Phase 1 terra firme, and nearly 206.8% the value for the number of diet items from all Phases of terra firme combined.,

Physical characteristics of fruits

Size, hardness, colour, number of seeds and mean percentage weight for the fruits were obtained for 249 species, 59 of which were eaten by *C. m. ouakary* and 190 of which were not. Tables V-5 and V-6 present a summary of the results, comparing characters of the whole fruit and the pericarp for eaten and non-eaten fruits. Table V-7 considers pericarp colour. I used χ^2 tests, to test whether the proportions of eaten and non-eaten fruits varied significantly from random for the various characteristics investigated. (The Bonferroni Correction to the p-values for significance for repeat testing with two categories is 0.025, with three 0.016, with four is 0.012 and with five categories is 0.01).

To further analyse for preference for physical characteristics in the diet of the golden-backed uacari, I used Ivlev's Index of Selectivity (*I*) (Ivlev, 1961), where:

$$I = (U-A) / (U+A)$$

Where *A* is availability (proportion of total no. in sample; eaten plus non-eaten) and *U* is use (eaten). Availability for each diet plant species was calculated as the proportion of the total number of species in the each phenophase (flower, fruit, new leaf) in the phenology study plots (Chapter 3). The resulting index gives values between 1 (total selection) and -1 (total avoidance). A zero value indicates the species is being eaten in a proportion that reflects its relative representation in the sampled environment.

Table V-5 Weight, Size and Seed number for Eaten and Non-eaten Fruit in Diet of Golden-backed Uacaris at Jaú

	Size (mm)				***Weight (g)***				***Seed number***		
	Small >50	***medium <10***	***large 11-24***	***very large 25-50***	***light <10***	***medium 11-50***	***heavy 51-100***	***very heavy >101***	***single***	***multiple 2-5***	***numerous >6***
Eaten No.	11 (21.5%)	14 (27.5%)	23 (45%)	3 (5.8%)	3 (5.8%)	3 (5.8%)	26 (50%)	20 (38%)	8 (17.8%)	13 (28.9%)	24 (53.3%)
Non-eaten No.	28 (16.2%)	60 (34.7%)	78 (45%)	7 (4%)	2 (5.4%)	4 (10.8%)	22 (59.5%)	9 (24.3%)	33 (20.7%)	15 (9.4%)	111 (69.8%)
Ivlev Value	0.14	-0.115	0	0.183	.035	-.301	-.086	.219	-.048	.509	-.134
χ^2 Values	*0.851* *d.f. = 7* *P = < 0.99, n.s.*				*1.576* *d.f. = 7* *P = < 0.95 n.s.*				*8.77* *d.f. 7* *P = < 0.1n.s*		

2 ***Table V-6 Physical Characteristics of Exterior of Eaten and Non-eaten Fruit in Diet of Golden-backed Uacaris at Jaú***

	Suture		***Hardness***				***Thickness (mm)***					***Defences***		
	Present	**Absent**	***Soft***	***Semi-hard***	***Hard***	***Woody***	***V. Thin < 0.4***	***Thin 0.5-1.0***	***Medium 1.1-2.0***	***Thick 2.1-3.9***	***V. Thick >4***	***None***	***Spines***	***Latex***
Eaten (N, %)	*19 (33.3 %)*	*38 (66.7 %)*	*10 (29.4%)*	*8 (23.5%)*	*11 (32.4%)*	*5 (14.7%)*	*13 (20.9%)*	*12 (19.35)*	*18 (29%)*	*13 (20.9)*	*6 (9.7%)*	*29 (37.7%)*	*3 (3.9%)*	*45 (58.4%)*
Non-eaten (N, %)	*50 (26.2 %)*	*141 (73.8 %)*	*12 (9.5%)*	*43 (34.1%)*	*17 (34.1%)*	*54 (42.8%)*	*15 (25.4%)*	*8 (13.5%)*	*15 (25.4%)*	*14 (23.7%)*	*7 (11.7%)*	*38 (22.4%)*	*11 (6.4%)*	*121 (71.2%)*
Ivlev Value	*.119*	*-.05*	*.511*	*-.184*	*-.002*	*-488*	*-.097*	*.178*	*.02*	*-.062*	*-.093*	*.254*	*-.42*	*-.098*
χ^2 Values	*0.866* *d.f. = 3* *P = < 0.95 , n.s.*		*15.68* *d.f. = 7* *P = < 0.05* **				*0.597* *d.f. = 9* *P = < .995, n.s.*					*4.66* *d.f. = 5* *P=<.0.1, n.s.*		

Table V-7: Pericarp Colours of Fruit Eaten and Non-eaten by Uacaris

No. (%)	*Pale*	*Green*	*Red*	*Dark*
Eaten N=57	0	37 (64.9)	6 (10.5%)	14 (24.6%)
Non-eaten N=141	32(22.7%)	57 (40.4%)	10 (7.1%)	42 (29.8%)
χ^2 Value, df = 3	20.973 P = < 0.001 ***			
Ivlev Value	-1	.232	0.193	-.009

From the χ^2 test results presented in tables V-5 - 7, it can be seen that for golden-backed uacaris at Jaú the differences between eaten and non-eaten fruits in criteria classes Colour, Defences, Seed Number, Size, Suture, Thickness and Weight are not significantly different. Statistically significant differences were recorded only for Hardness. However, though the lack of a comparable data set for uneaten fruit makes a χ^2 test impractical, it is notable that almost half of the fruits eaten have a high ratio of seed to total fruit weight.

Size of trees used in different phases

As seen (Table V-4, Appendix V-4), fruits of more species of tree were eaten in Phase 2 than in Phase 1 or 3. These came from trees that were, on average, larger than those in Phase 3. As tables V-1 to 3 and Appendix V-1 show, in Phase 1 in terra firme the main diet components were canopy giants such as *Bombacopsis* (Bombacaceae), *Chrysophyllum* and *Pouteria* (Spotaceae), and *Lecythis* (Lecythidaceae), plus the understory trees *Inga* (Fabaceae) and *Tocoa* (Melastomataceae) and *Astrocaryum* palms. During the same phase in igapó, canopy and emergent species from *Eschweilera* (Lecythidaceae), *Hydrochorea* (Fabaceae), *Mabea* (Euphorbiaceae), *Micropholis* and *Pouteria* (Sapotaceae) and *Swartzia* (Fabaceae) dominated the diet, but smaller trees such as *Buchenavia* (Combretaceae) and *Panopsis* (Proteaceae), with a vine, *Malouetia* (Apocynaceae), also important. In Phase 2, main contributors to the diet were canopy giants and emergents (*Mabea* [Euphorbiaceae], *Eschweilera* and *Micropholis* and *Pouteria*). The only shrub exploited at high frequency, *Eugenia gomesiana* (Myrtaceae), was common (Appendix III-1) and fruited briefly but abundantly. The uacaris eating its

soft, ball-like, fruits were mostly sub-adults. In Phase 3 the diet was dominated by non-fruit resources (Section 5.3.7), and those trees exploited for fruit were small understory species (*Guatteria* [Annonaceae], *Maprounea* [Euphobriaceae], *Casearia* [Flacourtiaceae], *Ternstroemia* [Theaceae]. This is further discussed in Chapters 6 and 7.

Use of lianas

Studies of the feeding ecology of *C. c. calvus* (Ayres, 1986a) and *C. m. melanocephalus* (Boubli, 1997a) indicated that seeds, fruit pulp and young leaves from lianas become increasingly important in the diet when little fruit is available on trees. For comparative purposes, I examined the proportional contribution of lianas to the diet of *C. m. ouakary*. Of the 136 identified plant taxa in the *C. m. ouakary* diet, 18 (13.2%) grew only as lianas. Fruit or leaves of seven liana species were eaten in Phase 1, of seven species in Phase 2 and of ten species in Phase 3 (two species were eaten in two Phases, one was eaten in all three). Table V-8 shows liana feeding records by Phase and diet category, Table V-9 shows these records as a proportion of the number of feeding records *per* Phase.

***Table V-8: Liana Feeding Records for* C. m. ouakary**

Phase	***Liana Feeding Records, N and % per category per phase***				
	Seeds (immature)	**Pulp**	**Flowers**	**Leaves**	**Totals (%)**
1	70 (57.9)	2 (1.7)	27 (22.2)	22 (18.2)	121 (15.4)
2	473 (98.1)	2 (0.4)	7 (1.5)	0	482 (61.4)
3	3 (1.6)	88 (48.4)	63 (34.6)	28 (15.4)	182 (23.2)
Totals (%)	546 (69.5)	92 (11.7)	97 (12.4)	50 (6.4)	785

Table V-9: Proportions of Liana-derived Items in Diet per Phase

Phase	***Total No. Feeding Records***	***No. Liana Feeding Records***	***Liana Records as % of Total Feeding Records per Phase***	***Liana Feeding Records, N and % per category per phase***			
				Seeds (immature)	***Pulp***	***Flowers***	***Leaves***
1	2452	121	4.9	70 (2.8)	2 (0.08)	27 (1.1)	22 (0.9)
2	7765	482	6.2	473 (6.1)	2 (0.02)	7 (0.1)	--
3	1685	182	10.8	3 (0.2)	88 (5.2)	63 (3.7)	28 (1.7)
Totals	11,902	785	6.6	546 (4.6)	92 (0.8)	97 (0.8)	50 (0.4)

The proportions of food categories for lianas were broadly similar to those of overall diet (Fig. V-2), with the notable absence of pith, and a slightly lower frequency of leaf use. Pulp was the only fruit-derived food category other than immature seeds. There was no notable peak in any Phases of the use of lianas for foods.

5.3.2 Feeding Behaviour Observations

Arboreal feeding – canopy and emergent layers

Differences in processing rates: Fruits with between one and three seeds were, with two exceptions, processed in < 15 seconds (Table V-10). Larger, multi-seeded fruit often took longer to open, but mean time per seed would have been less than for 1-3 seeded fruits.

Table V-10: Ranked Uacari Processing Times for Various Food Categories

Species	***Food Category***	***Processing Time (secs)***		
		N	***Mean***	***Range***
Eschweilera tenuifolia	Young leaves	10	1.2	1-2
Myrcia spp.	Fruit (≤ 2.5cm) greatest length, with 1-3 Seeds	6	2	1-3
Swartzia acuminata	Insect in refugium (rolled young lvs)	9	3.2	2-4
Eugenia spp.	Fruit (≤ 2.5cm) greatest length, with 1-3 Seeds	40	3.8	2-5
Lecythis pisonis	Insect in refugium (rolled young lvs)	10	3.9	3-5
Mabea nitida	Fruit (≤ 2.5cm) greatest length, with 1-3 seeds	23	5.3	3-7
Diospyros cavalcantei	Fruit (≤ 2.5cm) greatest length, with 1-3 seeds	3	5.66	5-6
Amanoa oblongifolia	Fruit (≤ 2.5cm) greatest length, with 1-3 seeds	88	5.7	3-8
Micropholis venulosa	Fruit (≤ 2.5cm) greatest length, with 1-3 seeds	22	5.8	5-7
Chaunochiton loranthoides	Fruit (≤ 2.5cm) greatest length, with 1-3 seeds	8	5.9	4-8
Laetia sp.	Multi-seeded Fruits	11	6.1	5-7
Endlicheria chalisa	Insect in shoot	4	6.25	5-8
Buchenavia ochrograma	Fruit (≤ 2.5cm) greatest length, with 1-3 seeds	76	6.36	4-9
Macrolobium acaciifolium	Fruit (≥2.5cm) greatest length, with 1-3 seeds	3	6.4	5-8
Clusia leprantha	Insect in petiole	7	6.6	5-8
Ormosia sp.	Young leaves	5	7.8	7-9
Pouteria elgans	Fruit (≤ 2.5cm) greatest length, with 1-3 seeds	17	8.6	7-12
Tontalea sp.	Pulp: Fruit (≤ 2.5cm) greatest length	19	11.2	9-14
Licania heteromorpha	Pulp: Fruit (≤5cm) greatest length	2	14.5	11-18
Swartzia laevicarpa	Aril: Fruit (≤5cm) greatest length	27	17.1	12-22
Heavea spruceana	Pith	23	18.7	14-24
Aechmea mertensii	Leaf bases	8	28.8	15-38
Heavea spruceana	Fruit (≥2.5cm) greatest length, with 1-3 seeds	10	27.2	17-38
Duroia velutina	Multi-seeded fruits	14	46.3	27-63
Eschweilera tenuifolia	Multi-seeded fruits	44	57.1	18-107
Inga obidensis	Multi-seeded fruits	4	40.5	19-76
Aldina heterophylla	Fruit (≥2.5cm) greatest length, with 1-3 seeds	18	62.8	43-88

Leaves were processed very quickly, but other non-fruit items generally required longer to process than fruit-based diet items (Table V-10).

How fruits were eaten: At Jaú fruits exploited by uacaris for their seeds were always dentally processed. I never recorded uacaris trying to open fruits by hitting them forcefully against trunks or branches, as recorded by Peres (1991a) for Amazonian *Cebus*, and by red nosed cuxiu (*Ch. Albinasus*: Liliam Pinto, pers. comm.), or by using tools as Mannu & Ottoni (2009) reported for *Cebus* from savanna-like Caatinga vegetation. Once the fruit had been obtained, fruits enough to require both hands for manipulation were always eaten in a sitting posture. Fruits used by uacaris at Jaú differed greatly in their physical properties (Tables V-5 - 7), and considerable variation was observed in how fruits were processed for their seeds. Eleven distinct processing modes were observed, four of which are shown in Fig. V-6:

1) fruit eaten entire (small Myrtaceae [*Calyptranthes*, *Eugenia* and *Myrcia*], young *Swartzia*, young *Astrocarium jauari*), N=660

2) canine used to directly extract seed, pericarp dropped (Fabaceae [*Inga* and *Parkia*], Memcylaceae, larger Myrtaceae, Polygalaceae [*Securidaca* sp.]), N=328

3) indehiscent fruit split longitudinally with one or both canines, seed (or aril) then removed with canines or incisors (Combretaceae, Fabaceae [*Aldina*, *Swartzia*], Sapotaceae [*Elaeoluma*, *Manilkarna*, *Micropholis*, *Pouteria*]), N=4388

4) indehiscent single-seeded fruit split transversely with canines, seed then removed with canines or incisors (Olacaceae [*Chaunochiton*], Theaceae [*Ternstroemia*]), N=298

5) indehiscent multi-seeded fruit bitten into two and the seeds extracted individually with incisors from the central axis of the ovary (Rubiaceae [*Duroia*]), N=183

6) small, sutured fruit with succulent pericarp, pericarpic suture opened with canine (Flacourtiaceae [*Casearia* and *Laetia*]), N=45

7) thick exocarp and or mesocarp of large, sutured fruit removed with incisors, suture on endocarp opened with canine (Apocynaceae [*Aspidospermum*], Euphorbiaceae [*Hevea*]), N=67

8) suture of pericarp of non-succulent sutured fruit opened direct with canine (Bombacaceae [*Bombacopsis*], Elaeocarpaceae [*Sloanea*], Euphorbiaceae [*Amanoa, Mabea*], Fabaceae [*Macrolobium*], Proteaceae [*Panopsis*], Sapotaceae [*Chrysophyllum*]), N=776

9) pyxidium opened at juncture of operculum and bowl (the pyxidial suture) by combination of (a) gnawing with incisors and then leverage and puncture with canines and or incisors once site of purchase has been created or (b) leverage and puncture by the canines or (b) leverage and puncture by canines at the pyxidial suture (Lecythidaceae [*Cariniana, Couratari, Eschweilera, Lecythis*] when nearly mature). Seeds removed with combination of digits and incisors, N=1067

10) pyxidium ripped open with puncture of single canine to middle fruit (Lecythidaceae [*Eschweilera* c.f. *romeu-cardosoi* or *wachenheimii*] when very young and pyxidial suture still tightly sealed), N=43

11) thin-walled pyxidia are snapped like a breadstick to reveal the alate seeds inside (Lecythidaceae [*Couratari multiflora*]). This form of foraging was encountered during preliminary visits (1999 and 2005), but not during the current study.

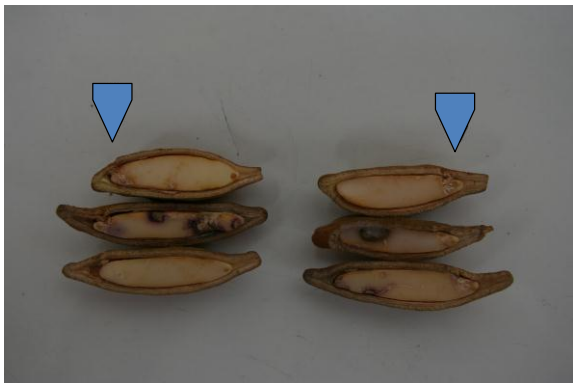
Type 3, *Manilkara*: incisor bite marks (arrowed) to remove seeds

Type 3, *Swartzia laevicarpa*, two-stage processing*:* pericarp opened with canines, and aril then extracted with incisors

Fig. V-6: Examples of Methods by which Uacaris Process Fruits

Type 5, *Duroia*, two-stage processing*:* fruit bitten in two with canines and seeds then extracted with incisors

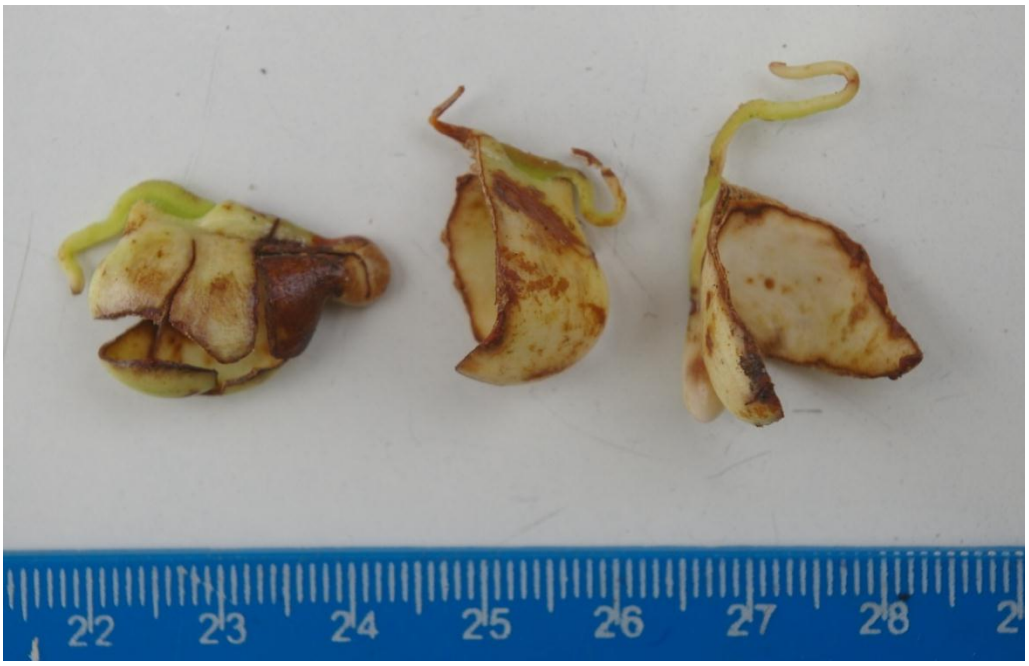
Type 7, *Aspidospermum*



Type 8, *Panopsis*, Arrows indicate locations of vertical bite mark on suture

Fig. V-6: Examples by which Uacaris Process Fruits (contd.) –1

Canines were also deployed with great precision, being used to slice open parchment-like endocarps of such species as Pau de Vidreo (*Byrsonima punctulata*: Malphigiaceae), *Buchenavia ochrograma*, *Lorostemon negrense* (Clusiaceae), and *Swartzia acuminata* to access the seeds inside (Fig. V-7), and to remove single seeds from soft berry-like fruits of Araça-sem-pé (*Mouriri guianense*: Memcylaceae) and Araça-boi (*Eugenia* spp.).



Swartzia acuminata (Fab.: Pap.), endocarp from young seeds

Fig. V-7: Precise Use of Canine: tannin-rich endocarps removed to access seed inside

Non-canopy feeding records in flooded igapó

On one occasion during Phase 3 three adult uacaris were observed in a dense part of the lower stratum of flooded igapó, suspending themselves by their ankles from the lowest hanging branches in order to reach floating Macucú (*Aldina heterophylla*: Fab.: Pap.) fruits that had become trapped in the mess of vertical stems and accumulated flotsam. Upon retrieving a pod from the water each animal then climbed to a larger higher branch where it sat and removed the thick (to 3cm) spongy pericarp before eating the seed. Animals were already engaged in this activity when they were encountered, and continued

for an additional 17 mins. until the local supply of accessible *A. heterophylla* appeared exhausted, except for very large fruits. All participating animals were of adult size. On other occasions both adult and juvenile-sized animals were observed foraging in bushes of the Mystaceae genera *Calyptranthes*, *Eugenia*, and *Myrcia*, and of *Casearia* and *Laetia* (Flacourtiaceae), all less than a meter from the water surface. These events occurred in Phase 3, when there were almost no fruits on trees or lianas, and the diet of the uacaris was dominated by leaves and pith.

In this context, it is notable that, on those rare occasions when *C. m. ouakary* was observed in understory and bushes in igapó, records of feeding on soft-fruited Myrtaceae almost always involved animals of sub-adult size (73 of 98 records: 74.4%), whereas all 36 observational records of *C. m. ouakary* feeding on the hard-fruited understory tree *Duroia* involved adult animals. In addition, during the Phase 3 fruit dearth, only adult animals foraged for the large hard pods of *Aldina* floating on the water surface in the flooded igapó.

In addition, the way in which uacaris bite their fruit foods could influence juvenile food species choices; providing it has force enough to break the pericarp, a primate feeding on pulp can take bites from the side of a fruit whether it has a large or small gape. On the other hand, feeding uacaris must generate a wide gape to permit the canine tips to be brought into contact with sutures. Clearly juvenile uacaris will have a smaller mouth, and so it may be that the diet of younger uacaris may to some extent be gape-limited it their choice of food items. It might therefore be predicted that not only might juvenile uacaris be eating more pulp, but also fruits that are smaller and or with weaker pericarps than adults. Age-size relationships where younger animals take smaller prey items are commonly recorded in the diets of fish (e.g. Puvanendran *et al.*, 2004) and reptile (e.g. Jayne *et al.*, 2002) species. In primates, maximum gape has been considered its influence on the ability of a species to practice gumivory (e.g. Viguier, 2004, Cheirogaleidae; Vineyard *et al*., 2003), on the speed and efficiency of loading food into the stomach (Nakayama *et*

al., 1999, *Macaca fuscata*), on the volume of food that can be attained with each bite (e.g. Shipley *et al*., 1994), and on what foods can physically be eaten (Anapol &. Lee, 1994, *Alouatta, Ateles, Cebus, Chiropotes, Saguinus, Saimiri*; Strait *et al*., 2009, *Australopithecus africanus*). However, the within-species differences attributable to ontogenetic differences in bite force accompanying different ages appear not to have been fully investigated to date. Even when such ontogenetic differences in gape size are examined, they tend to be analysed in terms of their roles as limiting factors in speed and efficiency of loading food into the stomach (Nakayama *et al*., 1999; Hanya, 2003, both *Macaca fuscata*). I have been unable to find material that has considered how juvenile diet might be limited in primates by gape size. Even Altmann (1998), in his detailed analysis of the feeding ecology of yearling baboons does not investigate this. He reports that processing time for legume pods decreases with age, but this is attributed to increased processing efficiency, resulting from enhanced manual dexterity, while the enhanced ability to access corms is attributed simply to greater body strength as the animals grow, nowhere are any foods considered to be excluded because of the animal's gape was insufficient.

Terrestrial feeding

Terrestrial feeding was directly observed in Phase 1. On six separate occasions over five days in Dec 2007 and Jan 2008 (27 feeding records), golden-backed uacaris were seen feeding on germinating seedlings in open areas of unflooded igapó. At a seventh site, uacaris were disturbed while feeding on the ground, but left before observations could be made. An additional two sites were found where field signs (e.g. still moist lacerations on seed testas, plumules cut, but fresh and unwilted) showed feeding had occurred very recently. Data was subsequently recorded from these areas. Species eaten for their seeds are detailed in Table V-11.

Table V-11: Records for Terrestrial Feeding by* Cacajao m. ouakary *on Germinating Seeds on Forest Floor of Dry Igapó.

Species	*No. Records*	*% of all Terrestrial Feeding Records*
Eschweilera tenuifolia	168	87.9
Leopoldinia pulchra	9	4.7
***Pouteria* 'Cabeçudo-1'**	8	4.2
Pouteria elegans	6	3.1
TOTALS	191	100

Uacaris fed on germinating seeds of four species, of which those of *E. tenuifolia* comprised the great majority (83.1%) of direct observational records. Five sample aggregations of *Eschweilera tenuifolia* seeds, showing no signs of having been visited by uacaris at the time of sampling, covered a mean of 2.6 m², with a mean density of 370.8 seedlings/m² (Table V-12). Of the 4858 seedlings counted in five sample patches, only 436 (8.9%) had more than the first set of leaves open. Only the seed was ever eaten, with the plumule and young leaves often being nipped off and discarded (Fig. V-8).

Germinating seeds eaten by *C. m. ouakary*

Patch of germinating seeds *in situ* (thin arrows). Clear central area is from uacari feeding (thick arrows)

***Fig. V-8: Terrestrial Feeding on* Eschweilera tenuifolia *seedlings by* Cacajao melanocephalus ouakary**

Table V-12: Size and Density of Patches of Germinating* Eschweilera *Seedlings

Patch No.	*Patch Size (m^2)*	*No. Seedlings*	*Seedlings / m^2*
1	1.8	536	297.8
2	2.2	1307	594
3	2.6	743	285
4	3.0	1246	415.3
5	3.5	1026	292.3
Means	**2.6**	**971.6**	**376.9**

Uacaris were only recorded feeding in large patches of seeds. The density of seeds in *Eschweilera* patches far exceeded the density of any other seedlings available at the time. Searches showed uacaris ate only seeds germinating within the patches. Also, while they ate small numbers of *Pouteria* and *Leopoldinia* (Arecaeae) were also present they did not eat germinating seeds of *Swartzia acuminata*, inflorescences of *Helosis* sp. [Balenophoraceae], and two types of fungus - one a species of *Clavulina* [Clavulinaceae: Order Cantharelles], the other unidentified).

Of seven *Eschweilera* patches at which uacaris had fed on germinating seedlings, two were close to thick overhanging lianas, two near large logs and three close to large buttress roots. During feeding, uacaris were observed to nip off and discard the shoots from the germinating seeds and just eat the seeds. Having eaten three or four seeds at the patch, they would them carry in their hands a variable number of additional seeds to a perch to eat (uacaris, like all Neotropical primates, lack cheek pouches). This perch was always off the ground and with a good view of the surrounding forest floor. Terrestrially foraging uacaris occured in groups numbering between two and five (N=6, mean 3.7 ± 1.36 SD). Lone uacaris were not observed foraging terrestrially (though one was observed to do so while another ate seeds on a nearby log). Fresh, wilted and very wilted nipped-off *Eschweilera* seedling stems were recovered from the same patch.

No member of a terrestrially-foraging group was ever observed acting as a sentinel. Individuals were hurried and jerky in their movements while on the ground and were clearly nervous. Uacaris appeared not to visit *Eschweilera* patches in dense vegetation even when they were close to those being exploited.

5.3.3 Selectivity Indices

Analyses of preference

Ivlev's Index of Selectivity (Ivlev, 1961) was used to analyse preference for species in the diet. For fruits, species with fewer than 20 feeding records were excluded from the analysis, as were those eaten species not registered in phenological study plots. Fig. V-9 shows the results for the remaining 36 species, while Table V-13 provides the resultant Ivlev values. For leaves, the twelve species displayed in Fig. V-10 represent all those species eaten for leaves that i) occurred in study plots, and ii) had more than five feeding records. Table V-14 gives their Ivlev values. The number of individual trees used for calculations was the number of individuals known to be reproducing. The number of plants in quadrats, the number reproducing, the number of fruit and leaf feeding records and the proportions used for the calculations are given in Appendix V-5.

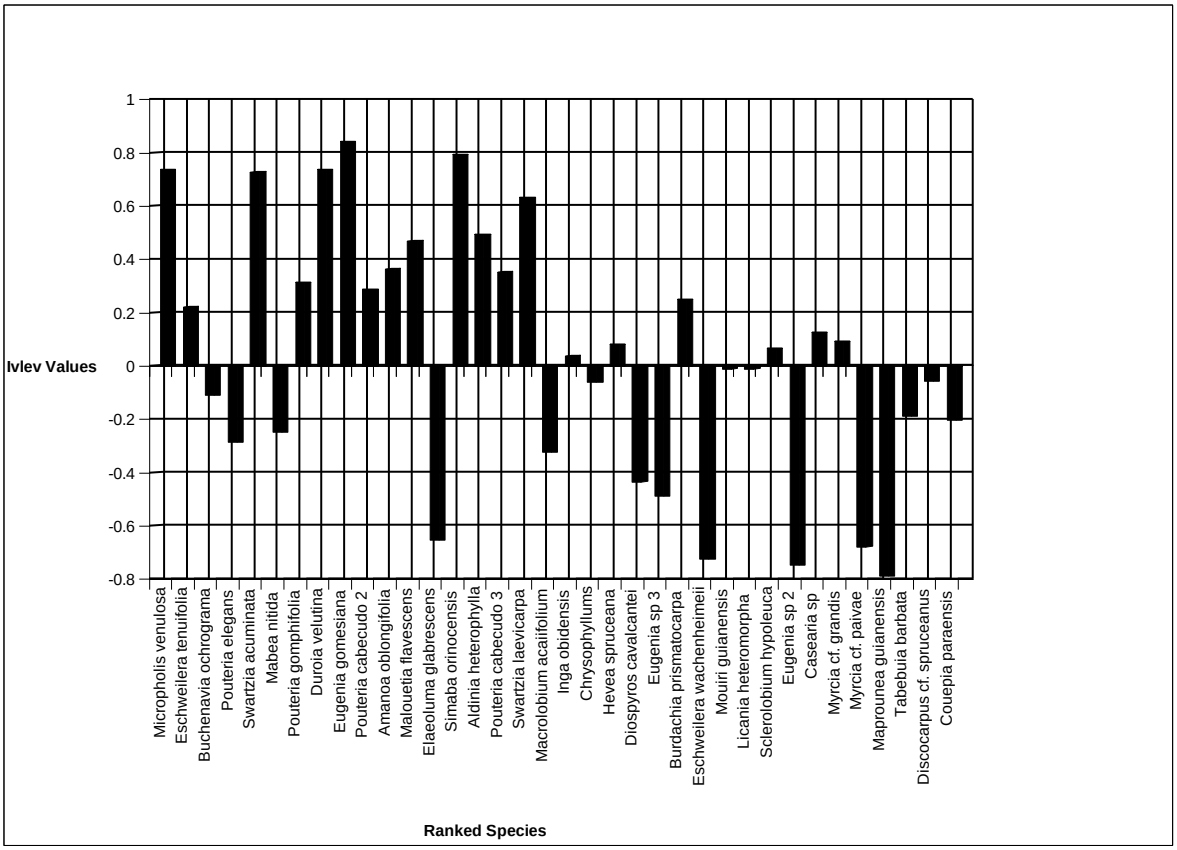


Fig. V-9 Ivlev Selection Ratios for Top 36 Species Eaten for Fruits

Table V-13: Species Eaten for Fruit / Seeds - Rank (No. Feeding Records) and Ivlev Values

Rank	Species	Ivlev Value	Rank	Species	Ivlev Value	Rank	Species	Ivlev Value
1	*Micropholis venulosa*	0.738	*13*	*Elaeoluma glabrescens*	-0.653	*25*	*Eschweilera wachenheimii*	0.251
2	*Eschweilera tenuifolia*	0.222	*14*	*Simaba orinocensis*	0.793	*26*	*Mouriri guianensis*	-0.726
3	*Buchenavia ochrograma*	-0.11	*15*	*Aldina heterophylla*	0. 495	*27*	*Licania heteromorpha*	-0.011
4	*Pouteria elegans*	-0.287	*16*	*Pouteria 'cabecudo' 3*	0.353	*28*	*Sclerolobium hypoleuca*	-0.011
5	*Swartzia acuminata*	0.728	*17*	*Swartzia laevicarpa*	0.632	*29*	*Eugenia* sp. 2	0.068
6	*Mabea nitida*	-0.248	*18*	*Macrolobium acaciifolium*	-0.324	*30*	*Casearia* sp.	-0.749
7	*Pouteria gomphifolia*	0.315	*19*	*Inga obidensis*	0.738	*31*	*Myrcia* cf. *grandis*	0.126
8	*Duroia velutina*	0.737	*20*	*Chrysophyllum s. sanguinolentum*	0. 038	*32*	*Myrcia c.*f. *paivae*	0.0918
9	*Eugenia gomesiana*	0.842	*21*	*Hevea spruceana*	-0.062	33	*Maprounea guianensis*	-0.678
10	*Pouteria 'cabecudo-2'*	0.287	*22*	*Diospyros cavalcantei*	0.081	*34*	*Tabebuia barbata*	-0.788
11	*Amanoa oblongifolia*	0.364	*23*	*Eugenia sp. 3*	-0.434	*35*	*Discocarpus* cf. *spruceanus*	0.189
12	*Malouetia flavescens*	0.469	*24*	*Burdachia prismatocarpa*	0.49	*36*	*Couepia paraensis*	-0.058

Of the 36 species most frequently-eaten for fruits/seeds, ten were strongly positively selected (≥ +0.4: Ivlev, 1961), five moderately positively selected (+0.2 to +0.39), six slightly selected (+0.01 to +0.19), five strongly negatively selected (≥ -0.4: Ivlev, 1961), four moderately negatively selected (-0.2 to -0.39), and six were slightly negatively selected (-0.038 to -0.189). None of these 36 species were eaten in exact proportion to their availability. The six most positively selected species (≥ +0.6) were among the top 18 species of the 36 species eaten for fruits/seeds., while four of the five most negatively selected species (≤+0.6) were in the latter 18 of this 36 species group.

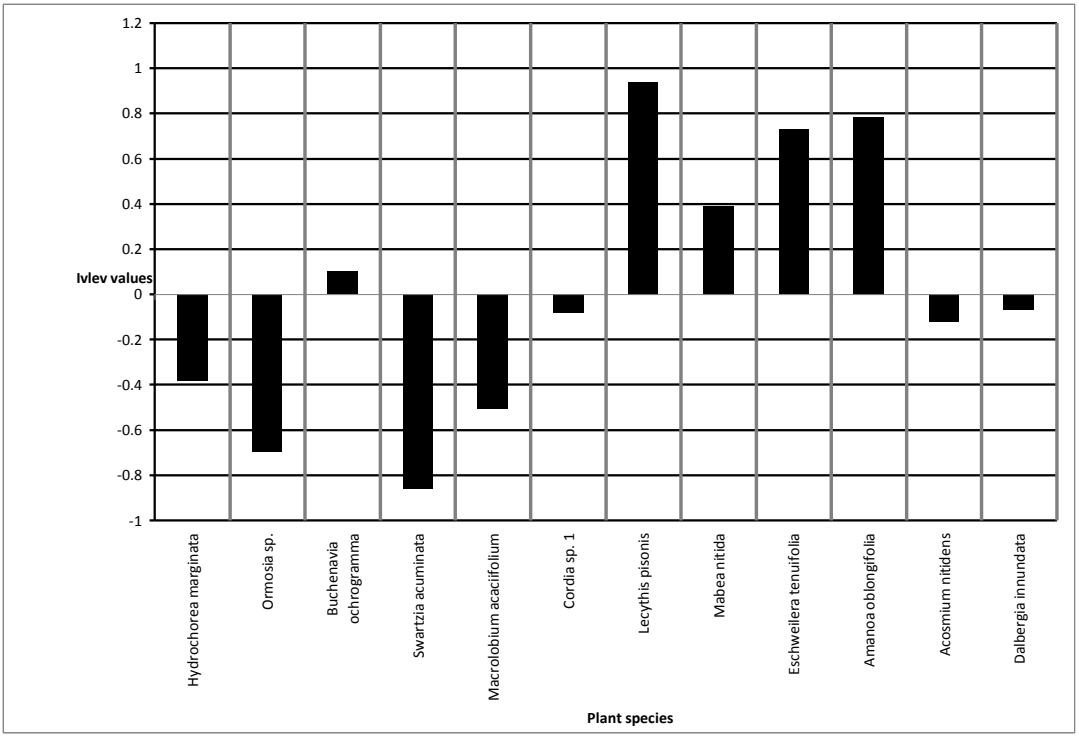


Fig. V-10: Selection Ratios for Top 12 Species eaten for Leaves

Table V-14: Species Eaten for Leaves - Rank (No. Feeding Records) and Ivlev Values

Rank	***Species***	***Ivlev Value***	***Rank***	***Species***	***Ivlev Value***	***Rank***	***Species***	***Ivlev Value***
1	*Hydrochorea marginata*	-0.381	*5*	*Macrolobium acaciifolium*	-0.506	*9*	*Eschweilera tenuifolia*	0.73
2	*Ormosia* sp.	-0.695	*6*	*Cordia* sp. 1	-0.081	*10*	*Amanoa oblongifolia*	0.782
3	*Buchenavia ochrograma*		*7*	*Lecythis pisonis*	0.094	*11*	*Acosmium nitens*	-0.124
4	*Swartzia acuminata*	-0.858	*8*	*Mabea nitida*	0.392	*12*	*Dalbergia inundata*	-0.068

Of the 12 species eaten for their leaves, four were strongly positively selected (≥ +0.4: Ivlev, 1961), one moderately positively selected (+0.2 to +0.39), two slightly selected (+0.01 to +0.19), one strongly negatively selected (≥ -0.4: Ivlev, 1961), one moderately negatively selected (-0.2 to -0.39), and three were slightly negatively selected. None of the top 12 species eaten for leaves were eaten in exact proportion to their availability. The four most negatively selected species were also among the six most frequently eaten

species, while the four most positively selected were distributed among the sixth and twelth most selected for leaves.

5.3.4 Handling and Processing Fruits

The use of sutures

The distribution of bite mark scars on fruit pericarps was scored for a total of 113 individual fruits from five different species of tree from Jaú's igapó forests. Table V-15 shows the results. The type of bite mark damage that was scored is shown in Fig. V-11.

Table V-15: Distribution of Uacari Bite Mark Scars on Fruits in Relation to Suture

Species	*N*	*Modal No. Bite Marks*	*Range*	*% on or Close to Suture[1]*	*% Elsewhere on Pericarp[2]*
Diospyros kono	20	1	1-2	100	0
Hevea spruceana	11	1	1-3	81	19
Mabea nitida	32	1	1-2	100	0
Macrolobium acaciifolium	27	1	1-2	100	0
Panopsis rubescens	23	1	1	100	0
Parkia discolor	14	1[3]	1	0	100

Note 1: [1] = bite mark directly on the suture, or within a distance from it that was ≤ 10% of fruit diameter;
Note 2: [2] = bite mark at a point on the pericarp whose distance from the nearest suture edge was > 10% of fruit diameter;
Note 3: [3] = one bite per locule, with number of seed-bearing locules varying from 8-16.

Intact fruit showing the 3 sutures characteristic of the Euphorbiaceae

Fruit showing initial preparation – incisal biting of the exocarp, canine insertion would then follow (sutures continue vertically through entire pericarp)

Fig. V-11: A Uacari Bite Along the Suture of a* Hevea spruceana *(Euphorbiaceae) Fruit

Table V-16 presents the force required (in Kg/mm²) to penetrate the pericarps of 65 fruits from five randomly chosen species of igapó tree whose fruit possessed sutures using a cast of a uacari canine mounted on a fruit penetrometer (sections 2.9.4 and 2.9.5).

Table V-16: Penetrability of Sutures and Pericarps of Five Uacari Diet Fruits

Species	***N***	***Penetrative Force (Kg/mm²) for Pericarp Suture (PS)***		***Penetrative Force (Kg/mm²) for Pericarp Body (PB)***		***Mean PS as % of Mean PB [1]***	***Mann-Whitney U-Test (PS cf. PB)***
		Mean	***Range***	***Mean***	***Range***		
Hevea spruceana	12	1.56	1.26-2.06	3.00	2.8-3.42	-48	Z=4.15692 P<0.001
Mabea nitida	24	2.1	1.6-3.1	3.4	1.7-3.8	-38.2	Z=4.65597 P<0.001
Macrolobium acaciifolium	11	5.46	4.8-6.2	3.54	2.7-3.2	+54.2	Z=4.93876 P<0.001
Panopsis rubescens	16	3.78	3.5-4.1	4.53	4.33-4.63	-17.3	Z=2.56285 P<0.01
Parkia discolor	12	5.16	4.18-5.8	1.19	0.83-1.54	+333.6	Z=6.35449 P<0.001

***Note**: [1]* PS-PB/PB

In all examined species the null hypothesis laid out in Section 2.9.5 is invalidadted and there is a significant difference between the penetrability of the pericarp at the suture and away from it.

Pentrability of infested vs. non-infested fruits

If perforated, a rigid structure suffers reduction in subsequent puncture resistance (Suknyov, 2000). Consequently, infested fruits might be included in the diet not so much because of the larvæ inside them, but because the pre-punctured pericarp is structurally weaker and so easier to penetrate with a bite (Borowicz, 1988). To test this possibility, using methods given in Section 2.9.7, I compared the penetrability of pericarps at the sutures of infested *vs.* non-infested fruits for two species of Euphorbiaceae species (*Amanoa oblongifolia* and *Mabea nitida*), and one Ebenaceae (*Diospyros cavalcanteii*).

All three were species consumed by uacaris at Jaú. Infested fruits were recognized by small holes bored into the pericarp by egg-depositing female insects, a feature absent in uninfested fruits (Fig. II-11). Results are given in Table V-17.

Table V-17: Differential Penetrability of Pericarps of Infested and Uninfested Fruits

Species	***N***	***Penetrative Force (Kg/mm²), Uninfested Fruit (UF)***		***N***	***Penetrative Force (Kg/mm²), Infested Fruit (IF)***		***Mean IF as % of Mean UF [1]***	***Mann-Whitney U-Test (UF cf. IF)***
		Mean	***Range***		***Mean***	***Range***		
Amanoa oblongifolia	11	3.91	3.1-4.6	25	3.01	2.7-4.1	-29.9	Z=5.02936 P<0.001
Diospyros cavalcanteii	9	3.38	1.8-4.5	8	2.65	1.5-3.8	-10.7	Z=1.39226 n.s.
Mabea nitida	25	4.15	3.25-4.8	25	3.6	1.25-4.8	-13.25	Z=2.39625 P<0.05

***Note**: [1]* IF-UF/UF

In all three cases the mean force needed to penetrate the pericarp of infested seeds was less than that for uninfested seed, and this is significantly different for *A. oblongifolia,* and *M. nitida,* indicating that, for these two species, the presence of insect-derived holes in the pericarp reduce its structural integrity, and lessens the amount of force needed to penetrate it. The presence of larval tunnels within the seed body could be a contributory factor. In total, I recorded infested fruits from 25 species, 24.75% of the 101 species recorded as being eaten for their seeds by golden-backed uacaris at Jaú. The species are listed in Appendix V-6. Of these, 12 had hard pericarps (species in bold), and for ten of these the modification of structural integrity could have had an effect on the penetrability of the pericarp. The other two, *Bombacopsis macrocalyx* and *Eschweilera tenuifolia,* had very thick pericarps and would probably not have been affected.

5.3.5 Microcarnivory

Free-ranging arthropods

Canopy arthropod abundances were not quantified and so selection ratios could not be calculated. Observations of uacaris feeing on free-ranging arthropods were rare, and because many igapó fish species are highly dependent on autochthonous material for food (Correa et al., 2007), such events were only infrequently followed by retrieval of fragments of the eaten invertebrate. In igapó, across all phases, uacaris fed on 25 taxa of free-ranging arthropods from 10 orders, and two classes, and including at least 15 families of insects. They were seen to feed on ants in leaf nests, free-ranging ants, beetle larvæ in rotten branches, caterpillars (large caterpillars, over 4cm long of a Saturniid moth, possibly *Automeris* [Hemileucinae], and others <2cm [unidentified]), fulgorid bugs (stripped from the exterior surface of pods of an Apocynaceae vine), grasshoppers (*Tropidacris* sp.: Acrididae, >10cm long and other smaller ones), mayflies (*Campsurus*: Polymitarcyidae, caught in disused spiders webs), spiders (free-ranging and on webs), termites (*Nausutermes* sp.: Termitidae, picked from branches, others [unidentified] plucked as alates from disused spider webs), and wasps (larvæ and adults of *Polybia*: Polistidae, taken from nests). Uacaris were also seen to attempt to grab butterflies and moths from the air with their hands, and to search piles of dead leaves.

Insect larvæ in fruits:

Twenty-five of the 101 species recorded in this study as being eaten by *C. m. ouakary* for their seeds had seeds infested by insects (24.75%). The species are listed in Appendix V-6. Fig. V-12 shows an infested fruit. I retrieved from five of these 25 species insect-containing seeds or fruit partly eaten by uacaris: *Calyptranthes* c.f. *creba* (N=3, Myrtaceae: Coleoptera larvæ), *Chaunochiton loranthoides* (N=8: Olacaceae: infested by

larvæ of the dipteran genus *Anastrepha*: Tephritidae), *Eschweilera tenuifolia* (N=17: infestated by clear-wing moths, family Sesoidea and micro-hymenoptera), *Macrolobium acaciifolium* (N=2, Fabaceae: Coleoptera larvæ), and *Sloanea* sp. (N=3, Elaeocarpaceae: Coleoptera, larvæ and adults). I estimated the contribution of insect larvæ to seed weight in fruits of *Chaunochiton*, *Eschweilera*, *Macrolobium* and of *Calyptranthes*, *Eugenia* and *Myrcia* (Myrtaceae). For the three taxa of single-seeded fruits (*Chaunochiton*, *Macrolobium* and combined Myrtaceae), the mean on-tree infestation rate was 49%. In such fruits, the mean percentage of seed weight from infesting insect was 45.9%.

Chaunochiron loranthoides (Olacaceae): infested (left), uninfested (right).
Four larvæ are present, one is arrowed.

Fig. V-12: Example of Insect-infested and Uninfested Fruits

Table V-18: Absolute and Proportional Weights of Insect Larvæ Infesting Seeds of Single Seeded Uacari Diet Fruits

Species	*N*	*N infested*	*% infested*	*N Larvæ per Fruit, Mean (Range)*	*Absolute Weight (g) of Larvæ per Seed, Mean (Range)*	*Larval Weight / % Fruit Total Weight (g), Mean (Range)*
Chaunochiton	48	21	43.8	4.2 (2 - 8)	0.97 (0.4 –2.1)	53.7 (30 – 86.7)
Macrolobium	50	14	22	1.2 (1 - 2)	3.7 (1.2 - 5.5)	39.7 (17.1 – 51
Myrtaceae*	24	9	37.5	1.3 (1 - 3)	0.85 (0.2 - 1.4)	44.2 (25 – 61.1)

* *Calyptranthes*, *Eugenia* and *Myrcia* combined due to in-field taxonomic difficulties.

Eschweilera tenuifolia ranks second in uacari feeding records for immature seeds (Section 5.3.1), and hence insect larvæ in the seeds could be an important souce of protein. I examined 86 pyxidia from which seeds had been eaten. Nine (10.5%) contained live larval insects, or seeds with larval insect damage (frass, cocoons, exit holes and/or tunnel bores in the pyxidial wall). I analysed five infested pyxidia removed directly from *E. tenuifolia* trees to test percentage infestation. Of the 144 seeds, 128 (88.9%) were infested (70.5-100% per pyxidium), with larvæ constituting a mean of 13% of the weight of infested fruits (range 7.5-27.5%).

Insect larvæ in leaves

In igapó, newly-unfolding leaves of arabá (*Swartzia acuminata*) trees were preyed upon by Tortricid moth larvæ which sealed shut the individual developing leaflets of the compound leaves with silk, eating the now-concealed upper lamella before pupating within the still living folded structure. Infestation was not universal, with only five of 27 *S. acuminata* trees bearing noticeable quantities of such leaves. These trees were visited by *Cacajao m. ouakary*, *Cebus albifrons* and *Cebus apella*, all of whom fed on the larvæ. Both *Cebus* spp. put entire leaflets into their mouth and then either ingested them whole or (after several leaflets) spat out a paste of masticated lamina. Uacaris slit open each leaflet dentally, extracted individual larvæ and then dropped the leaflet.

Recently-mature leaves of an igapó understory tree, cunhum liso (*Duroia aquatica*: Rubiaceae), hosted the larvæ of a Pyralid or Tortricid moth which welded two terminal leaves together and then fed on the upper (now inner) lamina before pupating. Infestation was sporadic, with 17 of 53 *Duroia* trees being infested (32.1%), but only four (7.5%) of these heavily. The uacaris pulled the paired leaves apart and picked off the moth larvæ with their fingers. While in terra firme forest, uacaris plucked the newly-emerging leaves

of sapucaia (*Lecythis pisonis*: Lecythidaceae), opening them to remove caterpillars eating the still-folded leaves.

Stem-tunneling insect larvæ

I also obtained three direct observations of uacaris eating stem tunneling insects: two in stems of *Pouteria 'cabecudo'* (Sapotaceae) and one in a leaf petiole of *Clusia* c.f. *leprantha* (Clusiaceae). An additional 71 instances were retrieved from feeding debris. The damage pattern was the same as those stems on which feeding had been observed and each was regarded a single feeding record. In these 71 records, stem boring insect larvæ were recorded from the young terminal stems of four species of tree (*Clusia* c.f. *leprantha*: Clusiaceae, *Hydrochorea marginata*: Fabaceae, *Endlicheira* sp.: Lauraceae, and *Pouteria 'cabecudo'*: Sapotaceae), and from the petioles of three further species (one Clusiaceae and two Sapotaceae: Appendix V-3).

5.3.6 Nectar and Flowers

How flowers were eaten

Uacaris at Jau were recorded eating the open flowers of 18 plant species, and the flower buds of a further three. For those flowers eaten when open, I never recorded the specific removal of anthers. Instead all species appeared to be opened near the nectary. The two most eaten species were both members of the Lecythidaceae: *Eschweilera tenuifolia* (434 feeding records) and *Couratari* c.f. *tenuicarpa* (187 feeding records). Of the 18 species eaten for their flowers, the pollination system was obtained for 17, of which two (both Annonaceae) were excluded because they were eaten for their petals alone. Of the remaining 15, 8 (53%) were bee-pollinated (*Clitoria javitensis, Codonanthe crassifolia, Couratari* c.f. *tenuicarpa, Distictella* sp., *Eschweilera tenuifolia, Passiflora costata, P. phellos, Tabebuia barbata*). All but two were diurnally pollinated. Only one species (*Tabernaemontana* sp.) was pollinated by birds. The remainder was pollinated by small

beetles and small flies (*Calyptranthes* sp., *Endlicheria* sp., *Mabea nitida, Philodendrom* c.f. *megallophyllum, Phoradodendron poeppigii, Piper* sp.).

5.3.7 Leaves, Leaf Bases, and Flower Stems

Leaves

Leaf consumption constituted 1298 feeding records, which were divided across five categories: leaf buds, leaf bases, young leaves, mature leaves, and leaflet junctions. Uacaris were recorded eating leaves of 31 species of tree, vine and liana, of which 22 were identified at least to genus (Appendix V-1). Images of eaten leaves are given in Fig. V-13. Leaves were eaten in four different ways: entire leaf (e.g. *Amanoa oblongifolia, Eschweilera tenuifolia, Mabea nitida*), distal half of leaf or leaflets (e.g. *Hydrochorea marginata, Buchenavia oxycarpa* and *B. ochrogramma, Codonanthe crassicaudata*), leaf base only (e.g. *Achmea mertensii, Scleria tentacissima*: Cyperaceae; *Trigonidium* sp.: Orchidaceae), and junction of compound palmate leaflets (*Hevea spruceana*). The majority of leaf-related feeding records (N=1084, 83.5%) were of young leaves. Of the 12 top ranked species consumed for leaves, six were Fabaceae. These six species contributed 55.6% of all leaf feeding records.

The manner in which leaves were processed by uacaris appeared very precise. For several species this may relate to latex avoidance by uacaris. To access leaves of the latex-rich genus *Pouteria* (Sapotaceae), uacaris broke off small stems and then plucked individual leaves from these, shredding each along the lamella, so that the central (latex-rich) vein was not broken (Fig. V-13, upper). With other species, latex avoidance was based on selectivity of species and phenological stage. Taquarí (*Amanoa oblongifolia*) and seringaí (*Mabea nitida*) are both from the latex-rich family Euphorbiaceae. In Aug uacaris ate young leaves and stems of taquari which, at this stage, do not give latex when

broken. With other species, latex avoidance was based on selectivity of species and phenological stage.

Mature Cabeçudo leaves (*Pouteria* sp.).

Young Tento leaves (*Sclerolobium* sp.)

***Fig. V-13: Leaves Eaten by* C. m. ouakary**

Taquarí (*Amanoa oblongifolia*) and seringaí (*Mabea nitida*) are both from the latex-rich family Euphorbiaceae. In Aug uacaris ate young leaves and stems of taquari which, at this stage, do not give latex when broken. Contemporaneous trees of seringaí more phenologically advanced and giving latex when either of these two parts was broken were not eaten at this time. Likewise, more mature, latex-rich, taquarí were later ignored.

With the mimosaceous legume tree pulero de pato (*Hydrochorea marginata*), uacaris broke off a section of stem in a manner that appeared to facilitate the easy consumption of its long feathery compound leaves. Feeding on these when newly flushed, uacaris bit off new individual shoots bearing 2-7 fresh leaves and ate individual leaflets by biting them half-way down the leaf. Uacaris also eat the very topmost unopened buds (sometimes with the first 2 or 3 small leaves) all in one bite. The shoots appear to have been bitten through to provide a food item that could be manipulated easily to access the leaves, since individual leaves themselves are almost too pliable to be eaten easily.

Leaf bases

The majority of records of leaf base feeding (N=77, 92.7% of records) came from the epiphytic bromeliad *Aechmea mertensii*. Uacaris would remove an entire plant from its tree branch and then, as with almost all items that could not be processed instantly, the animal would move to a new location before sitting down to pluck out individual leaves. The leaf bases were placed in the mouth and pulled across the incisors as a human does with the tegules of an artichoke. The single leaves were then discarded (Fig. V-14).

*Aechme*a leaves and inflorescence

Clump pulled from branch by uacari

Fig. V-14: **Achmea mertensii** ***(Bromeliaceae), exploited for leaf bases by*** **C. m. ouakary**

Flower stems

The eating of flower stems was recorded 11 times. All were from the bromeliad *Aechmea mertensii*. In each case, the last 2-3cm of the 13-17cm of the inflorescence stem was chewed once it had been pulled out of the centre of the epiphyte.

5.3.8 Pith

Uacaris at Jaú made extensive use of pith, eating the spongy insides of the fresh shoots from five species of tree: *Clusia* c.f. *leprantha*, *Endlicheria chalisa* (Lauraceae), *Hevea spruceana* (Euphorbiaceae), *Ormosia* sp. (Fab.: Pap.), and *Pouteria elegans* (Sapotaceae), with the majority of records (54 of 87: 62%) coming from *Hevea*. In *H. spruceana*, pith was extracted from new shoots whose growth always accompanies its annual leaf-flush (Maia, 1997). *Hevea* is renowned for abundant latex (Gentry, 1993; Metcalf, 1967), and new shoots are especially rich in resiniferous canals, with higher flow rates than elsewhere on the plant (Back, 2002; Metcalf, 1967). To circumvent this challenge to food resource access, uacaris moderated resin flow by breaking shoots in two places, then using their incisors to split longitudinally the area between the breaks before removing the pith with a canine (Fig. V-15).

Hevea spruceana (Euphorbiaceae)

Fig. V-15: Stem from which Pith Extracted (groove left by uacari canine arrowed)

5.3.9 Other Foods

Uacaris were observed on 17 occasions to bite dead wood and then, after processing, drop the branch. I collected two feeding records of uacaris feeding on fungi, when an animal in trees above dry igapó dropped two small fragments on which it had been feeding. It was identified as a member of the Order Agaricales, but of an unknown family. I did not see uacaris feeding on fungi in flooded igapó.

5.3.10 Fœcal Analysis

Individual fæcal pellets averaged 10x7x7mm, and a volume of some 490cm³ (N=65). Diet items were identified to order and, where possible, to family using a Leitz dissecting microscope. Every pellet analysed was of a pink-grey colour, with the material of the matrix very finely chewed and of an even paste-like texture. Fragments or parts from

seven arthropod orders were recovered from: Araneae, Blattoidea, Coleoptera (larvæ and adults), Hymenoptera (Formicidae), Isoptera, Lepidoptera (larvæ) and Orthoptera. Some additional material was recovered that may have been earthworm skin or from larval diptera, samples being too small for certain identification. The overall proportion of insect material varied from a trace to 11% (mean 5.3%) by volume of the individual fæcal pellet. Every analysed pellet contained some arthropod remains. Most material was highly comminuted, and fragments larger than 4 x 4mm were rare. Non-arthropod material included *Duroia* seeds, and broken fruits of the fur-dispersed sedge *Scleria tenacissima* ingested during grooming. There was no evidence of other plant material, nor of nematodes, cestoid proglottids or any other indication of intestinal parasitism. I did not observe fungal spores, pollen or lepidopteran wing scales. Ant and termite wings were few, suggesting most eaten ants were workers and not dispersing sexual castes.

5.4 Discussion

5.4.1 Comparison with other Pitheciines and other Primates

Previous studies

There have been three other extensive field studies of the diet of members of the genus *Cacajao* (Ayres, 1986a; Boubli, 1997a, Bowler, 2007). Aquino & Encarnación (1999) studied *C. c. ucayalii* diet, but restricted their focus to fruits only. Defler (2004) provides a list of the 20 top ranked diet species for *C. m. ouakary* in Colombia. Table V-19 lists the proportions of diet items for previous studies of *Cacajao*, and those from studies of two other pitheciine genera, *Chiropotes* and *Pithecia*. Diet data from *Ateles, Lagothrix* and *Cebus* spp. are included for comparison. Table V-20 provides a more detailed comparison of the fruit component of the diets.

Table V-19: Proportions of Diet Categories for Cacajao, other Pitheciines and Additional Selected Neotropical Primates

Species	*Author*	*% fruits and seeds*	*% flowers & nectar*	*% leaves*	*% fauna*	*% other*	*N species*	*Notes*
C. c. calvus	Ayres (1986a)	85.3	6.2	3.3	5.2	0	83	100 spp. used across 18 months
C. c. ucayalii	Bowler (2007)	91.22	3.72	1.69	2.82	0.56	164	
C. m. melanocephalus	Boubli (1997a)	91	4	3	2	0	120	
C. m. ouakary	**This study**	**78.8**	**7.2**	**10.8**	**2.4**	**0.8**	**174**	
Ch. albinasus	Pinto (2008)	93.4	5	0	0.9	0.6	125	
Ch. chiropotes	Veiga (2006)	75.6	12.3			12.1	147	
Ch. satanus	Ayres (1981)	72.5	11.4	(16.1) *	0	0	85	*Includes leaves and insects
Pithecia albicans	Peres (1993)	80.2	8	9.5	0.4	0	81	
P. pithecia	Setz (1987, 1994)	81	8	11	0	0	190	
Ateles b. belzebuth	Nunes (1998)	91.7	0	8.3	0	0	--	,
Ateles p. paniscus	van Roosmalen (1985b)	82.9	6.4	7.9	0.4	2.76	207	
Lagothrix cana	Peres (1994b)	67.4	3.1	16.2	<1	13.4	--	
Lagothrix poeppigii	Di Fiore (2004)	75.5	3.5	9.8	9.3	1.9	--	
Cebus olivaceus	Robinson (1986)	46*	3	6**	33	12***	66	*only 5 species of fruits eaten unripe (10% of total) ** includes buds and shoots *** includes drinking

Note: *Aquino & Encanación (1999)' s study of the diet of* C. c. ucayalii *was excluded because it covered only fruit.*

Table V-20: Percentage of Fruit Sub-categories in Total Diet of Selected Neotropical Primates

Species	***Author***	***%* Immat. Fruit**	***%* Immat. Seeds**	***%* Mature Fruit**	***%* Mature Seeds**	***%* Pulp**	***%* Aril**	***% non-Fruit***	***Notes***
C. c. calvus	Ayres (1986a)	0	66.9	0	0	(18.4)	(18.4)	14.7	1
C. c. ucayalii	Bowler (2007)	0	50.56	0	1.01	38.52	1.13	8.78	
C. c. ucayalii	Aquino & Encarnación (1999)	0	3.7	0	40.7	51.85	3.7	--	2, 3
C. m. melanocephalus	Boubli (1997a)	0	63.8	0	14			22.2	4
C. m. ouakary	**This study**	**0**	**68.3**	**4.2**	**0**	**3.1**	**3.2**	**21.2**	
C. m. ouakary	Defler (2004)	93		0		7		0	5
Chiropotes albinasus	Pinto (2008)	0	48.2	0	6	39.2	0	6.6	
Chiropotes chiropotes	Veiga (2006)	13.1	50.5	9.4	0	0	0	27	
Ateles b. belezebuth	Nunes (1998)	3.2	0	88.5	0	0	0	8.3	4
Ateles p. paniscus	van Roosmalen (1985b)	3.7	0	83.45		0		12.85	5
Lagothrix cana	Peres (1994)	0.8	0	66.6	0			32.6	4
Lagothrix poeppigii	Di Fiore (2004)	4.2	0	71.3	0			24.5	4

***Notes*: 1,** Pulp and aril reported as combined categories. **2**, % species, not feeding records. **3**, Only fruits and seeds studied. **4**, Pulp and arils used but %s not reported. **5**, Some mature fruits eaten whole, some arils eaten, but these categories not separately enumerated. Immature seeds and immature fruits not reported separately.

Tables V-19 and V-20 shows that it is common for Neotropical primates to eat a variety of diet items, with all of the broad-spectrum studies registering items being eaten in each of the five categories delineated above. There are significant differences, however: while the use of fruit is high in Atelines and Pitheciines (Table V-19), the two lineages use the resource in markedly different ways (Table V-20), with Atelines eating almost entirely ripe fruit and its pulp, while Pitheciines mostly eat seeds and primarily immature seeds. Where pulp contributes a large percentage of the diet (e.g. *C. c. ucayalii*: Aquino & Encarnación, 1999; Bowler, 2007), this is due to study populations using a locally superabundant resource, the fruit of the palm *Mauritia flexuosa*. This situation may not be representative of the diet of the sub-species as a whole.

Comparing the diet of *C. m. ouakary* at Jaú with other published studies, it can be seen that the diet is highly species diverse in comparison to some studies (e.g. Ayres, 1986a; Boubli, 1997a). The current study has also recorded around one-third more plant families than any other previous study of *Cacajao* diet (e.g. Boubli, 1996, 32 families, 37.5% more; Bowler, 2007, 33 families, 33.3% more). The recorded diet at Jaú also appears unusual in that it includes three times more leaves than any heretofore reported for the genus *Cacajao*, as well as the highest proportion of flowers for any uacari so far studied. Correspondingly, the diet of *C. m. ouakary* at Jaú has the lowest proportion of immature seeds of any *Cacajao* taxon so far investigated. With the exception of *Ch. satanus* studied by Ayres (1981), the levels of leaves in the diet also exceed those recored for any *Chiropotes* so far investigated. The level of faunivory is unexceptional, being within the range of other studies of both *Cacajao* and *Chiropotes.* In the overall proportions of the diet, *C. m. ouakary* at Jaú has a compositional profile more like *Pithecia* than other larger members of the family. However, this similarity may be more apparent than real: even under varying suites of seasonal resource availability, monthly *Pithecia* diets commonly contain a mixture of flowers, seeds and fruits, in which the latter two are near-equally represented (e.g. Norconk, 2006, 2007; Peres, 1993; Setz, 1987, 1994), while for *C. m. ouakary*, leaves are poorly represented in most months and the high proportion of leaves (at least relative to other uacari studies) in the mean annual diet comes from a short period of the year during which this resource dominated the diet (Fig. V-3: Section 5.3.1).

Annual variation in diet diversity

The number of overall diet species for *C. m. ouakary* is greatest in Phase 3 igapó, where 91 species were recorded (Table V-4). Phase 3 is when there is the lowest availability of fruits and seeds. The tendency for animals to eat fewer individual items from a greater

number of species in those seasons of lower availability of preferred resource is a common pattern; in addition to primates (Hill, 1999: *Macaca fuscata*; Galetti & Pedroni, 1994: *Cebus apella*), this response has been recorded for many other taxa (including: bears, Munro *et al.*, 2006; deer, Arnold & Drawe, 1979; hummingbirds, Cotton, 2008; stoats, Martinoli *et al.*, 2001; tropical freshwater fish, Deus & Petrere-Junior, 2003; and small frugivorous tropical birds, Levey *et al.*, 1984). It is a response predicted from optimal diet theory (Estabrook & Dunham, 1976; Sih & Christiansen, 2000).

Annual variation of use of non-plant diet items by uacaris

Fruits in the immature stage are available for up to four times as long as fruits in the ripe stage (Norconk, 1996). For primate species that feed on seeds of unripe fruit this should provide a smoothing out of resource availability, permitting them to avoid the resource bottlenecks that frequently affect ripe fruit feeding primates (Norconk *et al.*, 1998). However, because of the highly seasonal nature of igapó, where fruit production is tied to the flux in flood water levels, a dearth in fruit availability does occur (Phase 3), and so *C. m. ouakary*, despite being a highly-specialized predator on immature seeds for much of the year, spends some months eating both leaves and non-plant items.

Uacaris appear to track the availability of fruit resources and to respond to the changes in proportional availability of the various fruit species (Section 5.3.1 and Chapter 6). Could this also explain the higher incidence of insectivory in the dry season (Phase 3) diet? Currently any answer to this question must be inferential as seasonal variation in overall insect densities is unknown for Jaú or for any other igapó site. However, Guerrero *et al.* (2003) compared dry and rainy season arthropod densities from Sapotaceae and Lecythidaceae crowns at a terra firme site near Manaus (220km east of Jaú, but in the same climatic region, with the same broad rainfall and phenological patterns). They

found little difference in absolute numbers between the two seasons (118,076 dry season individuals *vs*. 138,353 wet season individuals, a 14.7% increase). However, it is important to consider spatial patterning: lepidoptera larvæ will be available only when the host plant is in the appropriate phenophase, making periods of leaf flush (Phase 3 in igapó) the peak period for their availability. Other insect groups, such as wasps, spiders, ants and termites are more likely to be available throughout the year. Such broad patterns were reported by Guerrero *et al*. (2003). As might be predicted from such mosaic availability, feeding records for caterpillars are all from Phase 3 (dry season), which is the season of their peak availability, while those insect types that are available all year have scattered records across all three phases. Thus it seems that uacaris are responding to the abundance of Lepidoptera larvæ, but feeding fortuitously from other orders.

Comparison with previous studies

The uacaris at Jaú follow the general pattern of the genus *Cacajao* of having an annual diet dominated by seeds from unripe fruit (tables V-19 and 20). However, the diet of *C. m. ouakary* at Jaú is somewhat unusual because of the peaks of consumption of non-seed items when immature seeds are not available (tables V-2 - 4, appendices V-1 - 4). Diet items for which a primate does not appear to be specialized to exploit behaviorally, morphologically or physiologically are often termed fall-back foods (Lambert, 2010; Robbins *et al*., 2006), and their exploitation most commonly occurs at times when other major components of the diet are not available (e.g. Yamagiwa & Basabose, 2006).

For *C. m. ouakary* at Jaú, the use of young leaves as a diet item (Phase 3) seems to fit this classification as fall-back foods. New leaves comprised 95.2% of the foliage eaten. Folivory occurs in *C. c. calvus, C. c. ucayalii*, and *C. m. melanocephalus* but in small or relatively low percentages (3.3, 1.7 and 3.3%, respectively), whereas in *C. m. ouakary* it

constituted nearly 11% of feeding records. The records for other *Cacajao* species (Ayres, 1986a; Bowler, 2007; Boubli, 1997a) are, like *C. m. ouakary*, dominated by new leaves. However, the use of leaves as a fall back food is not as clear cut in *C. calvus* and *C. m. melanocephalus* as it is in the *C. m. ouakary*. Though present in the diet, there is no reported seasonal peak in their use and leaves never dominate the diet of *C. c. calvus* or *C. m. melanocephalus* in the way that they do the diet of *C. m. ouakary* at Jaú in Phase 3. This may well be because the habitat types in which these other uacaris have been studied have plant communities in which the annual patterns of new leaf production differ markedly from the strongly peaked phenology of igapó at Jaú.

At Jaú, as in igapó generally, the flush of new leaves is concentrated into a single peak that is both highly time-restricted and nearly ubiquitous across the flooded forest plant community (Parolin *et al*., 2002). However, such a phenological pulse does not occur in várzea and terra firme where *C. c. ucayalii* has been studied (Bowler, 2007), nor in caatinga sites where Boubli (1997a) observed *C. m. melanocephalus*. In these habitats, leaf flush has a broad temporal spread, and so, for *C. c. ucayalii* and *C. m. melanocephalus*, at no time of the year are new leaves the dominant resource available for consumption.

The situation for *C. c. calvus* studied by Ayres (1986a) at Lake Teiú-Mamirauá, is slightly different: while a strong peak in new leaf production occurs, it almost exactly coincides with a peak in immature fruits, *C. c. calvus'* principal diet item (Ayres, 1989). At Teiú-Mamirauá there would appear to be no part of the annual cycle in which fruiting trees did not make up at least 10% of the plant community, leaving no period when young leaves were a dominant element in the resource profile. Ayres did not observe *C.*

c. calvus ingesting any leaves during his study. The only folivory records were germinating seedlings in the stomachs of two shot animals. In contrast, in Jaú Phase 3, the period of *C. m. ouakary*'s greatest leaf use, both the diet and the habitat of the golden-backed uacari had almost no fruit at all.

Characteristics of fruits

The Ivlev analysis of choice, and the Chi-squared tests, both indicated that *C. m. ouakary* displayed very little preference among the measured fruit characteristics, there only being a slight preference for fruits that were very hard (woody). There was no preference for fruits with or without sutures, but fruits with a high seed weight/total fruit weight ratio were preferred. Size, weight, pericarp thickness, and number of seeds were not influential and the presence or absence of defences also had no effect. This maybe because the powerful jaws of the uacari can cope with the extremes of sclerotization and pericarp hypertrophy encountered in most fruits of the region, while the lack of preference for fruit size and weights betokens a foraging strategy that focuses on whatever is maximally available and most abundant, irrespective or its size or weight. Ayres (1989) presented data on the proportions of various classes of fruit in the diet of *C. c. calvus* and found that most fruits chosen for their immature seeds were in the 10-100g range and that smaller fruits were rare in the *C. c. calvus* diet. However, as the proportions in the diet were not compared with those generally available in the habitat, it is not possible to say if this was the result of preference or chance. However, Ayres considered these proportions to be due to behaviours to maximize effective handling costs, with stripping pericarps being proportionally more difficult on smaller fruits while working larger pericarps provided more reward per unit effort. Unlike *C. m. ouakary*, however, the diet of *C. c. calvus*, did include a substantial proportion of species with yellow or white pulpy pericarps. Bowler

(2007) did not present an analysis of pericarp colour for the diet fruits of *C. c. ucayalii*, but did note that of the top 10 fruits in the diet of *C. c. ucayalii* six were classifiable as 'hard' or 'very hard'. In the total diet of *C. c. ucayalii*, 2% of feeding records were soft fruits, 47% were medium fruits, 18% hard, and 7% very hard. These data are based on individual fruits, not species and so the large number of records in the medium category is due to the predominance in the Yavarí *C. c. ucayalii* diet of the pulp of the *Mauritia flexuosa* palm. Boubli (1997a) found that the majority of fruit eaten by *C. m. melanocephalus* were of medium hardness, animal dispersed, and green. Though fruit up to 32cm in length were eaten, the majority (46.5%) of fruit in the diet of *C. m. melanocephalus* reported by Boubli, were small (1-5cm). This may be due to the low percentage of hydrochorous species in the *C. m. melanocephalus* diet (5.8%).

Thus, allowing for the variation in habitat (the várzea of *C. c. calvus*: Ayres, 1986a; the caatinga of *C. m. melanocephalus*: Boubli, 1997a), and in the prominence in the diet of one particular species (*C. c. ucayalii*: Bowler, 2007), there is a remarkable concordance in the fruit parts and stages of fruit maturity that the four long-term studies of uacari diets have so far registered. While the proportions of fruits to other diet categories might vary somewhat (tables V-19 and 20), and the families concerned can be very different (next section), the actual types of fruit parts eaten and the maturation stages at which this occurs remain essentially the same, underscoring the specialist nature of the *Cacajao* niche across habitats and the breadth of the western Amazonian basin.

Important plant families

Table V-21 summarizes the most important three plant families from twelve diet studies of eight species of Pitheciines. Here, across 11 alphabetically ordered plant families, the three most important plant families from each study of pithecine diet are indicated by the

presence of the study code number in one of each of the three ranked columns. This means of presentation has been chosen as it demonstrates where the study numbers cluster and so shows the relative importance of the various families across the rankings.

Table V-21: Comparison of the Top Three Families from 12 Studies of* Cacajao *and* Chiropotes *Diets

Family	***Studies in which Ranked 1st (see below for Key to study numbers)***	***Studies in which Ranked 2nd.***	***Studies in which Ranked 3rd.***
Apocynaceae			1
Arecaceae	2, 6, 11	12	
Burseraceae			13
Euphorbiaceae	5		
*Fabaceae**		1,5, 11	2, ***4*** ,6, 12
Hippocrataceae			3
Lecythidaceae	3, 13	***4***, 7, 9, 10	
Loranthaceae		8	
Moraceae		3	7, 8, 9, 10, 11
Sapotaceae	1, 2, ***4***, 7, 8, 9, 10	6, 13	5
Simabouraceae	12		

Key to studies: 1= Aquino & Encarnación (1999: *C. c. ucayalii*), 2 = Ayres (1981: *Ch. satanus*), 3 = Ayres (1986a: *C. c. calvus*), ***4***= Barnett (this study: *C. m. ouakary*), 5 = Boubli (1997a: *C. m. melanocephalus*), 6 = Bowler (2007: *C. c. ucayalii*), 7 = Frazão (1992: *Ch. sagulatus*), 8 = Peetz (2001: *Ch. chiropotes*), 9 = Pinto (2008: *Ch. albinasus*), 10 = van Roosmalen *et al*. (1988: *Ch. sagulatus*, reported as *C. satanus chiropotes*), 11 = Silva (2003: *Ch. satanus*), 12 = Veiga (2006: *Ch. chiropotes*, Gp 1), 13 = Veiga (2006: *Ch. chiropotes*, Gp 2).

Looking across the 11 families, it is apparent that, by favouring Fabaceae, Lecythidaceae and Sapotaceae, uacaris at Jaú are making choices very similar to those made by most pitheciines. In terms of both density and species diversity, these are three of the commonest Amazonian plant families (Gentry, 1988; Mori & Lepsch-Cunha, 1995; ter Steege *et al*., 2006). Moraceae, another family favoured by many Pitheciines, were barely represented in Jaú feeding records (3 species, 14 feeding records total). This reflects the fact that, while fig species and their allies are common in Amazonian forests (Berg *et al*., 1984; Gentry, 1998), they have both low abundance and small diversity in igapó (Chapter 3, and Parolin *et al*., 2002). Arecaceae were the prime family in three

studies, with a single species (Buritĺ, *Mauritia flexuosa*) dominating the diet of the *C. c. ucayalii* studied by Bowler (2007), and highly represented in the diet of another three studies (Table V-21). Yet at Jaú palms were a minor diet item, with a total of 28 feeding records across three species (ranked 27th. of 45 families). This may be explained partially by the absence of any stands of *M. flexuosa* in either the study area itself or its immediate vicinity. However, while not recorded in the feeding ecology of the population in the current study, golden-backed uacaris elsewhere in Jaú are known to eat the pulpy mesocarp of buritĺ, leaving igapó and crossing substantial tracts of terra firme to reach the stands (Barnett, 2005; Barnett *et al*., 2005b).

The uniformities in diet items also continue to below the level of the family. In the Sapotaceae and Lecythidaceae, for example, there is remarkable consistency across the studies of genera most frequently recorded as diet items. For example, in the latter family, *Eschweilera* is an important food source for many pithecine species including *C. c. calvus*, *C. c. ucayalii*, *Ch. albinasus*, *Ch. satanus* and *Ch. sagulatus* (Ayres & Prance, in press; Pinto, 2008). Where the method of processing is mentioned, there are also strong similarities in how items are processed. Van Roosmalen *et al*. (1988), for example, describe how *Ch. sagulatus*, when accessing the seeds of *Eschweilera corrugata* and other members of the genus, bites a hole at the juncture of the pyxidial bowl and its operculum, 'and then uses its procumbent incisors rather like a can opener to pop off the operculum and gain access to the seeds inside' (p. 14). As mentioned in Section 5.3.2, this is exactly the same stereotyped movement with which *C. m. ouakary* has been observed to process the pyxidia of *E. tenuifolia*. As van Roosmalen *et al.* point out, this

very efficient action allows very rapid access to fruits that less specialized primates (*Ce. apella*, for example) take far longer to open, if at all.

Selection ratios

Selection ratios provide a ranked index of how a study population is collectively investing to securing a particular diet item from the suite of diet items available. It estimates choice *via* summed foraging activities: but it does not provide an indication of how important any particular plant might be to its consumer. Ranked selection ratios rarely correspond to ranked percentage contribution to diet because not all species have equal abundances. So, for golden-backed uacaris at Jaú, while the most-eaten species, the comparatively rare sapotaceous tree *Micropholis venulosa* (41 trees in sample plots) had a selection ration of 0.788, the second most eaten, the lecythid *Eschweilera tenuifolia* had the fourth lowest positive selection ratio (0.222) because it was one of igapó's three most abundant trees (137 individuals in sample plots). In consequence, whilst *E. tenuifolia* is very important in the diet, it is so common that it is used only a little more than in direct proportion to its relative abundance in the tree community. In addition, a particular plant might be of vital importance when little else is available, but it is difficult for selection ratios to be subtle enough to reflect this. Thus selection ratios are rather blunt instruments, which do not provide a measure of how important a resource might be, just the relative amount of energy and time expended in securing it.

It is, nevertheless instructive to compare selection ratios for other *Cacajao* and for *Chiropotes* to see the extent of the time-energy investments that are made to obtain specific food items. Whilst there are some methodological differences in the ways selection ratios were calculated, and these are of a nature which might result in an

underestimation of the selection ratios of certain key species, the differences do not appear so great as to invalidate cross-site comparison.

Like *C. m. ouakary*, the ratios for some of the most important fruits most eaten by *C. m. melanocephalus* at Pico de Neblina (Boubli, 1997a) are very low (especially *Eperua leucantha*, *Heavea brasilensis*and *Micranda sprucei*, all < 0.1). As with *E. tenuifolia*, *Pouteria elegans* and *Buchenavia ochrograma* in the current study, these are three of the ten commonest plants in the caatinga inhabited by the population of *C. m. melanocephalus* studied by Boubli (1997a). The study of the Pico de Neblina caatingas *C. m. melanocephalus* (Boubli, 1997a) found that some genuinely rare trees (e.g. *Caryocar pallidum*: Caryocaraceae) were the focus of great attention and so received a high selection ratio. The current study observed a parallel situation with *Mouriri guianensis* (Memycelaceae). For *C. c. ucayalii*, Bowler (2007) observed a similar relationship; common genera like *Eschweilera*, *Licania*, and *Mauritia* were sufficiently abundant that their selection ratios were very small in comparison to their actual importance in the diet.

A number of factors that might influence diet item choice so that the proportion of plants in a primate species' diet does not exactly mirror the proportionate composition of the plant community in which it lives. Aspects that may lead to positive selection include: proportionately large crop volumes, presence of micronutrients, medicinal properties, proportionately high levels of a dietary element (e.g. crude protein) in critically limiting supply at the time (Doran-Sheehy *et al.*, 2006; Herrera & Heymann, 2004; Pruetz, 2006; Solanki *et al.*, 2008). Aspects that may lead to negative selection include: presence of commensal ants, gums and latex, spines, and chemical defences (Freeland & Jansen,

1974; Krishnamani, 1994; Oates *et al*., 1980; Stanford, 1991). These aspects have yet to be fully investigated for uacaris, but are clearly a fertile region of future research.

In this context, it is interesting to note that Bowler (2007) lists *Buchenavia* among the genera that were common but ignored by *C. c. ucayalii* uacaris at his Lago Preto study site. Two species were eaten at Jaú, once of which, *B. ochrograma*, was ranked third in selection ratios for both fruit and leaves. Combretaceae are known to be toxin-rich (Frone & Pfänder, 2004), which may support Glander (1982)'s view of that detoxifying abilities may not be equal across a primate genus. This has certainly been shown to be true for some mammalian genera (e.g. *Neotoma*: Sorensen *et al.,* 2004; where the specialist herbivore *N. stephensi* absorbs far fewer plant toxins than does the more generalist *N. albigula*). However, species confronted with a diet rich in toxins tend to modify meal size and feeding frequency to minimize total daily intake of toxins, and hence (Sorensen *et al.,* 2005a,b) the proportion of their total energy budget expended on detoxification, as a result of increased hepatic activity (Lamb *et al.,* 2004). Thus, it is possible that *Buchenavia* was avoided not because of its absolute toxicity to red uacaris, but because it was relatively too toxic at the time to be included in an optimal diet in which the energetic costs of detoxification are an important consideration. The investigation of such possibilities should encourage new lines of research in uacari foraging ecology.

5.4.2 How Uacaris Eat

Forest strata

The upper two layers of the forest are those which uacaris use most, with over 88% of observations coming from them. Of the 109 species of trees and palms contributing to the diet in the current study, 70 (64.2%) were members of these two upper strata when mature and fruiting. However, uacaris at Jaú were rarely recorded spending longer than

five minutes in the canopy of any one tree, which may well limit foraging opportunities. It is currently unclear why golden-backed uacaris spend so little time foraging in one patch before moving on to the next.

Use of canines

It was noted (Section 5.3.2) that, with several plant species, uacaris used their canines to separate delicately seed coats from the underlying seed before jettisoning the seed coat, and eating the seed (Fig. V-7). Such acts increase processing time and often require considerable manipulative skill (Norconk *et al*., 1998). However, these tissues are frequently rich in tannins and other defensive chemicals (e.g. Beninger & Hosfield, 2003; Janzen, 1971). Tannins, especially, are known to combine with dietary proteins and reduce their digestability (Chung-MacCourbrey *et al*., 1997; Robbins *et al*., 1987; Singleton, 1981). Thus, it is presumed that the time invested in removing seed coats is repaid by greater digestive efficiency and enhanced energetic gain *per* unit foraging time. Investigating this aspect in the field is only limited by the large samples of seeds required to obtain suffecient volumes of seed coats for analysis.

Use of sutures

Foraging studies have revealed that animals often process diet items in ways that maximize energetic gain, while minimizing processing time and muscular expenditure (Chivers *et al.*, 1984; Emlen, 1966; Garber, 1987; Hemingway, 1999; Hohmann, 2009; Milton, 1979, 1980, 1984; Sayers, 2008). Uniquely among primates (Kinzey, 1992), members of the pithecine genera *Pithecia, Chiropotes* and *Cacajao* use their canines, rather than molars, to open seeds (the pitheciine fourth genus, *Callicebus*, shows substantially fewer specializations for sclerocarpic foraging: Norconk, 2007). In *Cacajao*, the large, splayed canines (Fig. I-2) leave a characteristic bite mark. Table V-16 (Section

5.3.4) showed that the force required to penetrate the pericarp at the suture can be substantially less than that required to penetrate other parts of a fruit's surface. To gain access to seeds within, uacaris at Jaú penetrate such fruit as *Hevea spruceana*, *Mabea nitida* and *Panopsis rubescens* at the suture. Such bite specificity not only diminishes the risk of fracture and the extent of ablation of the end point of the canine, but reduces the energy that must be expended in making a bite. Feeding observations made during the current study suggest that, during the peak period of immature seed ingestion, a golden-backed uacari might process some 400 sutured seeds a day. Clearly, as Juanes (1992) and Mitcheli (1995) noted in a similar context for decapod crustaceans and Peter and Rosemary Grant have explored for Galapagos finches (e.g. Grant, 1999; Weiner, 2000), any saving in energy expended in each bite can have enormous cumulative effect on the energy budget, as well as substantially reducing the risk of damage to the major means by which these animals secure their food (in the primate's case their canines and incisors).

Species using pressure or puncture to process prey often deploy strategies that minimize the possibility of damage to the actuating part (e.g. Smallegange *et al.*, 2008: *Carcinus maenas* Portunidae, Decpoda). Alone among primates Pitheciines use the tips of their canines to open fruits (Todd Rae, pers. comm.; Kinzey, 1992). Accordingly, using fruit sutures to access seeds might also serve to reduce the chance of these key parts becoming fractured or broken.

That a fruit is bitten at the suture if one is present, appears to be a general rule of *C. m. ouakary* fruit processing. The two exceptions to this rule, *Macrolobium acaciifolium* and *Parkia discolor*, provide an interesting insight into the dynamics of bite force optimization in *C. m. ouakary*. The fruit of the legume *M. acaciifolium* is a single seeded

pod, in which the junction of the two valves is greatly thickened along the adaxial suture. Elsewhere, on the fruit the junction of the valves at the abaxial suture measures little more than 0.5mm, but at the base it exceeds 1.5mm and is much more lignified (Fig. V-16). Whilst the distal parts of the valves meet at a fine point, the more lignified adaxial suture forms a rise-and-groove structure at which the groove is the width of the tip of a uacari canine (Fig. V-16). Thus, though thicker, the adaxial suture provides greater purchase for canine insertion, a feature which may well reduce the processing time for each individual fruit. It may well be, therefore, for these two reasons, that all investigated 64 *M. acaciifolium* fruits had bite marks in the thicker part of the suture, even though it took more actual force to break through the pericarp at this point.

The adaxial suture is also greatly thickened in the leguminaceous genus *Parkia*, but here there is no prominent groove. It therefore requires less force to open the pericarp at the pod's side, where it is < 0.3mm thick, and barely sclerified. In all 15 examined pods of *P. discolor*, seeds had been extracted by breaking open the pod wall rather than entering *via* the suture. A photograph in Heymann (1990) shows that *C. c. calvus* in Peru display an identical behaviour when accessing seeds in *Parkia oppositifolia* pods.

Uacaris also bit into the thinnest part of the pericarp of many species lacking sutures, including *Buchenavia*, *Lorostemon* and *Pouteria*, indicating that minimizing penetrability is not confined to the perceivable groove in the pericarp surface. Mechanical considerations may also influence uacari choice of infested fruits, which require less force to open and so may provide younger smaller animals in sclerocarpically foraging species with access to otherwise unobtainable foods.

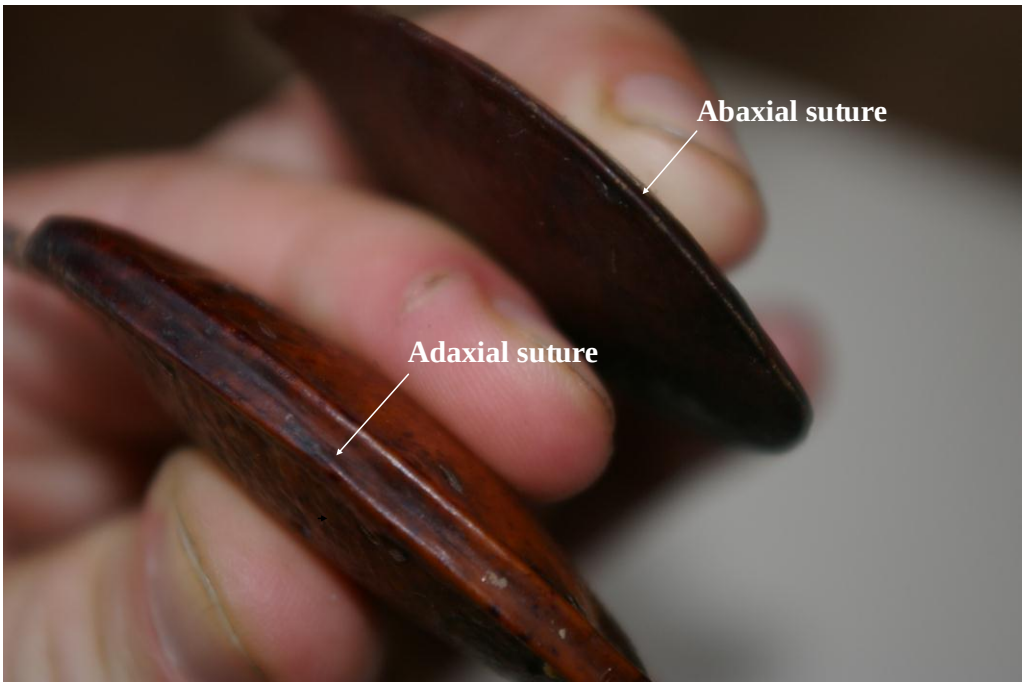


Fig. V-16: Fruits of* Macrolobium acaciifolium *(Fab.: Caes.) Showing Differences in Form of Adaxial and Abaxial Suture

Uacaris also bit into the thinnest part of the pericarp of many species lacking sutures, including *Buchenavia*, *Lorostemon* and *Pouteria*, indicating that minimizing penetrability is not confined to the perceivable groove in the pericarp surface. Mechanical considerations may also influence uacari choice of infested fruits, which require less force to open and so may provide younger smaller animals in sclerocarpically foraging species with access to otherwise unobtainable foods.

Bowler (2007: for *C. c. ucayalii*), and Boubli (1997a: for *C. m. melanocephalus*) both observed smaller uacaris being unable to open fruits readily tackled by adults, and considered the younger animals' smaller jaw muscle mass and lesser bite force responsible (see also Section 5.3.2, p. 233). A rigid structure suffers reduction in

subsequent puncture resistance if perforated (Suknyov, 2000), so infested fruits may be easier to break into than uninfested ones of a similar size. This could make them more attractive to smaller animals and so infested fruits may enter the diet not so much because of the larvæ inside them but because the pre-punctured pericarp is structurally weaker and so easier to penetrate (Borowicz, 1988). While I recorded that tunnels bored by insects into the pericarp of the fruits from three species of igapó tree lowered their penetrability to a prosthetic uacari canine mounted on a fruit penetrometer, ease of opening may not be the whole story. A higher incidence of infested fruits in the diet of younger animals, for example, might also be associated with increased protein requirements associated with growth (Herrera & Heymann, 2004).

For three species (*Parkia discolor, Inga obidensis* and *I. rhynchocalyx*, all Fab.:Mim.), uacaris behaved as if they were actively avoiding infested seeds present in developing pods. In each case, infested seeds were left in the pod, while none of the individual cells from which seeds had been extracted showed any signs of infestation (i.e. pod inner wall discoloration, presence of frass and/or exit holes). Chemical changes by seeds that attempt to poison invading insects, and/or chemical repellents produced by the infesting larvæ (Janzen, 1971, 1978; Sallabanks & Courtney, 1992) could both combine to make such infested seeds unpalatable an investigating uacari.

5.4.3 The Size and Frequency of Uacari Food Trees

In terra firme, none of the six most abundant species were recorded as being eaten by uacaris. However, in igapó, species important in the uacari diet (e.g. *Eschweilera tenuifolia, Pouteria elegans, Buchenavia ochrogamma, Mabea nítida, Eleoluma glabresecens* and *Hydrochorea marginata*), are also the most common species in the quadrats, and also in the combined analysis (‘all-igapó’ of Table III-1). They are not,

however, the largest trees (Table III-3). So, in igapó, uacaris are selecting the commonest, not the largest trees as sources of fruits. Yet, in terra firme, diet species like *Chrysophyllum sanguinolentum* (Sapotaceae) have both large trunks (100cm+) and canopies, but are not among the largest trees in the forest. The combination of high evenness and widely dispersed individuals in the terra firme, contrasts with the situation in igapó. This makes it possible that uacaris may have to remember the position of and actively seek out individual fruiting terra firme trees, while in igapó the relative abundance of species with edible fruits means that simply keeping moving is enough to fulfill daily food requirements. This could be tested with multi-annual comparisons of the trees used by uacaris in igapó and terra firme, and also is relevant to group size comparisons between the two habitats (Section 6.3.2 and Table VI-2), and to mean travel times between feeding sites.

5.4.4 Pentrability of Infested Fruits

The ten diet species whose hard pericarps would have had their structural integrity reduced by insect infestation constituted 12.9% of the seed feeding records and 8.8% of the feeding records of the overall diet. So the observed diminuition could have an important effect in diminishing the amount of energy expended in bite force by an animal on a daily and annual basis.

5.4.5 What Else Uacaris Eat

Uacaris have been generally considered to be seed predators (Norconk, 2007). However, in the current study nearly 20% of the recorded diet of *C. m. ouakary* came from other plant parts, these, and the role of arthropods, are considered here. In addition, the role of lianas and their fruits in the diet of *C. m. ouakary* is compared with that of other uacaris.

Plant parts

● flowers: Specific removal of anthers was not noted for any of the 18 flower species which golden-backed uacaris were observed to eat at Jaú. Instead all species appeared to be opened near the nectary. This suggests that all flowers were being eaten for their nectar, and not for the protein in the pollen. Primates may become nearly entirely florivorous for short periods, with the flowers used often being exploited both for their energy-rich nectar and for the protein-rich pollen (e.g. Jones, 1983: *Alouatta*; Lappan, 2009a: *Hylobates*; Muchlinski & Overdorf, 2001: Indriidae and Lemuridae; Riba-Hernandez & Stoner, 2005; *Ateles*). For most species, uacaris plucked flowers from their pedicels and processed them in the tree canopy in which they were encountered. *Codonanthe crassifolia* (Gesneriaceae), a small tree trunk living vine, was an exception. This vine is associated with the nests of *Camponotus* and *Crematogaster* ants (Kleinfeldt, 1978; Weber, 1943), who construct their nests among the roots. To a human the sting of these ants is quite a painful one (A. Barnett, pers. obs.). Uacaris at Jaú would nip off a flower-bearing stem and take it some distance away to process the flowers, and this may well be an attempt to avoid the ants' aggressive defensive responses.

Within the genus *Cacajao*, florivory has been reported for *C. c. calvus* (four species: Ayres, 1986a), *C. c. ucayalii* (four species: Bowler, 2007), *C. m. melanocephalus* (two species: Boubli, 1997a), and *C. m. ouakary* (one species: Defler, 2004). For *C. c. calvus*, monthly flower consumption (principally *Eschweilera turbinata*, for nectar) peaked at nearly 58% of the diet when little fruit was available (Ayres, 1986a, 1989). Flowers of *Eperua leucantha* (Fab.: Pap.) were the paramount diet item for *C. m. melanocephalus* during Oct-Dec, but declined in importance once unripe fruits of this leguminaceous tree

began to appear (Boubli, 1997a). The situation strongly parallels that of *C. m. ouakary* and *E. tenuifolia* which occurs in Phase 2. Florivory has also been reported for other Pitheciines, e.g. Pinto (2008: *Ch. albinasus,* 15 species, 5% of diet), and van Roosmalen *et al*. (1981: *Ch. sagulatus,* 6 species, 4.6% of diet). Table V-22 collates data on plant species whose flowers *Cacajao* species have been reported to consume. Because many of the reported ingestions were considered to be for nectar and because nectar concentrations vary with types of pollinator (Chalcoff *et al*., 2006; Krömer *et al*., 2008), pollinator type is included as a proxy for likely nectar concentration and volume.

Table V-22: Flower Species in Diets of Uacari Species, and their Pollinator Types

Plant Species	***Pollinator Type***	***Uacari Species***	***Author***
Bombax sp. (Bombac.)	either bats or birds	*C. c. calvus*	Ayres (1986a)
Clitoria javitensis (Fab.: Pap.)	bee	*C. m. ouakary*	Current study
Couratari c.f. *tenuicarpa* (Lecythidaceae)	bee	*C. m. ouakary*	Current study
Codonanthe crassifolia (Gesneriaceae)	bee	*C. m. ouakary*	Current study
Calyptranthes sp. (Myrtaceae)	various	*C. m. ouakary*	Current study
Distictella sp. (Boraginacae)	bee	*C. m. ouakary*	Current study
Duguettia sp. (Annonaceae) petals only	flies	*C. m. ouakary*	Current study
Endlicheria sp. (Lauraceae)	flies, beetles	*C. m. ouakary*	Current study
Eschweilera tenuifolia (Lecythidaceae)	bees	*C. m. ouakary*	Current study
Eschweilera turbinata	bee	*C. c. calvus*	Ayres (1986a)
Eschweilera sp.	bee	*C. c. ucayalii*	Bowler (2007)
Eschweilera sp.	bee	*C. m. ouakary*	Defler (2004)
Eperua leucantha	unknown[1]	*C. m. melanocephalus*	Boubli (1997a)
Guatteria sp. (Annonaceae) petals only	flies, beetles	*C. m. ouakary*	Current study
Gustavia hexapetala (Lecythid.)	bee	*C. c. calvus*	Ayres (1986a)
Gustavia sp.	bee	*C. c. ucayalii*	Bowler (2007)
Hydrochorea marginata (Fab.: Mim.)	unknown	*C. m. ouakary*	Current study
Mabea nitida (Euphorbiaceae)	flies, beetles	*C. m. ouakary*	Current study
Moronobea coccinea	bird	*C. c. ucayalii*	Bowler (2007)
Pachira insignis (Bombac.)	bat	*C. m. melanocephalus*	Boubli (1997a)
Parkia nitida	bat	*C. c. ucayalii*	Bowler (2007)
Passiflora costata (Passifloraceae)	bee, butterfly	*C. m. ouakary*	Current study
Passiflora c.f. *phellos* (Passifloraceae)	bee, butterfly	*C. m. ouakary*	Current study
Philodendron c.f. *megallophyllum* (Arecaceae)	flies, beetles	*C. m. ouakary*	Current study
Phoradendron poeppigii (Viscaceae) entire young unopened inflorescence	small flies	*C. m. ouakary*	Current study
Piper spp. (Piperaceae) entire inflorescence	wind, small bees, hoverflies	*C. m. ouakary*	Current study
Tabebuia sp. (Bignon.)	bee	*C. c. calvus*	Ayres (1986a)
Unidentified liana	?	*C. c. calvus*	Ayres (1986a)

[1] Cowan (1975) gives bats and moths as pollinators for other members of the genus

The majority (6 of the 9 species for which the pollinator is certain) of flowers that *C. m. ouakary* ate are bee-pollinated, with bird-pollinated species rare in the diet. Bee pollination is not the commonest syndrome in the Neotropics, where a substantial portion of the trees are pollinated by butterflies, flies, beetles, bats or birds (Bawa *et al*., 1985; Consiglio & Bourne, 2001; Fischer & Leal, 2006). Consequently, the uacari preference for bee-pollinated species is notable and very likely to be a consequence of the more concentrated nectar that bee-pollinated flowers possess in comparison with the nectars of those pollinated by birds (e.g. Gentry, 1974; Lange & Scott, 1999), or butterflies (e.g. Pivnick & McNeil, 1985).

Neither the current study, nor those summarized in Table V-22, registered uacaris eating the flowers of such ornithophilous species as *Aechmea, Epiphyllum, Moronobea* or *Psittacanthus.* Bird-pollinated flowers have nectar that is less concentrated than that of insect-pollinated species (Nicholson, 2002), which may explain why the flowers of common bird-pollinated genera such as *Aechmea*, *Epiphyllum* and *Moronobea* were not visited by uacaris. *Psittacanthus* is an abundant plant at Jaú, and has very large bunches of showy flowers. However, members of the genus are generally pollinated by very small hummingbirds (Azpeitia & Lara, 2006; Barnett, pers. obs.), and so, in addition to the nectar being sugar-weak, it is also present in low volumes. Flowers of other species also lack rewards. For example, *Clusia* flowers were ignored even when they were in fully open and uacaris were visiting the trees to feed on insects in the leaf petioles. This is likely to be because *Clusia*'s substantial flowers are nectarless, attracting Euglossine and Meliponine bee pollinators with waxes, resins and essential oils used by the bees in nest construction (Kaminsky & Absy, 2006). Reinforcing the idea that pollinator type may

influence whether or not the flowers of a species are eaten (or not) by uacaris, is the fact that several common tree species whose flowers were not eaten by *C. m. ouakary* are pollinated by nocturnally-active animals such as bats (*Caryocar glabra*: Bawa *et al*., 1985; *Parkia discolor*: Hopkins & Hopkins, 1992), or sphingid moths (*Himatanthus bracteatus*: Plumel, 1991). The absence of these species from the uacari diet may be explained by the tendency of such plants to provide nectar which is copious but dilute (Baker *et al.,* 1998), and available only at night (e.g. Pettersen & Knudsen, 2001; Tschapka & von Helversen, 2007).

The situation of *Eschweilera* flower-feeding presents an interesting example of intra-site variation. *Eschweilera turbinata* was reported by Ayres (1986a) as the highest ranked flower species in the diet of *C. c. calvus,* while Bowler (2007) reported flowers of *E. albiflora* (under their synonym *E. paucifolia*) to be eaten by *C. c. ucayalii.* Yet at Jaú, *E. albiflora* was never recorded in the diet of the golden-backed uacari, even though it was present in igapó. Instead, the conspecific *Eschweilera tenuifolia*, which ranked highest for number of feeding records for flowers, was consumed. This may be explained by varience in phenology of the two species, and the consequent differences in resources panoramas against which their availabilities are set. Flowering is highly seasonal in igapó at Jaú (Section 3.4) and *Eschweilera tenuifolia* trees flower between Dec and Feb (Parolin *et al*., 2002). This constitutes Phase 1 in Jaú, a period when, due to the lack of new leaves or fruit (figs. III-10, 11), there are very few resources available in igapó. At this time, igapó has little fruit and the large, nectar rich bee-pollinated and abundant flowers of *E. tenuifolia* (Fig. II-7) can provide an important energy source for uacaris returning from terra firme to the igapó. By contrast, Jaú's *E. albiflora* population flowers

in Jul-Aug (late Phase 2, early Phase 3). In Jul fruit is still available; in Aug the flush of new leaves begins. So, the availability of other edible resources at Jaú may be being masked, as the flowers of *E. albiflora* are overshadowed in availability by resources of other classes. In addition, relative rarity may be a factor: while *E. tenuifolia* is one of the commonest trees in igapó, *E. albiflora* is a rare tree at Jaú which probably contributes to its flower availability being masked by fruit abundance, and the abundance of flowers of other species. A similar situation may occur for the relatively rare *Arrabidea* cf. *nigrescens* (Bignoniaceae) which, like all members of the genus (Yanagizawa & Maimoni-Rodella, 2007), has flowers that are pollinated by large bees and which produce abundant nectar. However, at Jaú, *A.* c.f. *nigrescens* flowers at the same time as the much more abundant and larger bignon *Tabebuia barbata* in whose favour it may therefore have been ignored by flower-seeking uacaris.

● germinating seeds: Though most Amazonian mammals can swim (Goulding, 1989), the presence of floodwaters seasonally prevents terrestrial mammals from foraging in igapó until those 2-3 months of the year when the waters recede and the forest floor is exposed. This period is one of intense germination activity (Parolin, 2001a,bc), and rodents, deer, tapir and peccary all enter igapó to feed on this bonanza (Bodmer *et al.,* 1998, Haugaasen & Peres, 2005a,b; Barnett, unpublished observations). Predators, like jaguar, enter to feed on the herbivores (Barnett & de Castillho, in prep.). Thus, though foraging terrestrially may reduce the risk from aerial predators such as harpy eagles (which are known to attack uacaris: Barnett *et al*., in press), it is not a risk-free enterprise.

As seeds mature, their water content tends to decline, while the carbohydrate, fat and protein content proportionately increase (Laboriau, 1983; Silvertown, 2009). Terrestrial

foraging by *C. m. ouakary* for germinating seeds was recorded both in the current study, and for *C. c. calvus* by Ayres (1986a). Ayres (1993) noted that, at the Lake Teiú-Mamirauá study site, there is little terrestrial mammalian activity, either carnivore or herbivore, when the várzea forest-floor is exposed during low water, the implication being that in this period was comparatively safe for generally arboreal *C. c. calvus* to descend to the ground to forage. However, given the observations on *C. m. ouakary,* the association with a risk-related foraging strategy, as implied by Ayres, may be less important, and the prime driver, at least at Jaú, may well be the presence of abundant high quality food at the time when few other protein sources are available. Terrestrial foraging was reported neither for *C. m. melanocephalus* in Pico de Neblina, Brazil, nor for *C. c. ucayalii* at Lago Preto, Peru (Boubli, 1997a, and Bowler, 2007, respectively). It may be significant that in both areas the temporal patterning of in-canopy fruit availability is such that tree-borne fruit is present year-round, and this may well negate the need to descend to the ground to feed.

● leaves: Fabaceae's dominance of leaf feeding records (Section 5.3.7) may be associated with the tendency for leaves of this family to be high in nitrogen and low in fibre. This combination has led to their selection by a number of other seasonally folivorous primates, including several species of *Colobus* (McKey *et al*., 1981; Moreno-Black & Bent, 1982; Mowry *et al*., 1996).

In a prescient study, MacLarnon *et al*. (1986) analysed primate gastro-intestinal allometry and found indications that both *Cacajao calvus* and *C. m. melanocephalus* could be foliage eaters, because the enlarged hind gut indicated a diet of a low digestibility. At the time the study did not concord with what little was known of uacari

feeding biology, all of which indicated that uacaris ate little or no vegetation (Ayres, 1986a, 1989), an opinion that subsequent studies of *C. m. melanocephalus* (Boubli, 1997a) did little to change. However, as both preliminary work at Jaú (Barnett *et al*., 2005), and the current fuller study have shown, leaves can be of great seasonal importance for at least one species of the genus *Cacajao, C. m. ouakary*. Unlike birds (Biebach, 1998; McWilliams & Karasov, 2005), primates are not known to alter the relative proportions of their digestive system in response to seasonal changes in diet. If this general rule is adhered to by *Cacajao,* then the possession of a gastro-intestinal system partially suited to folivory, may in some way compromise the digestive efficiency of *C. m. ouakary*, making it less efficient at processing fruits and seeds than its less folivorous congeners *C. calvus* and *C. m. melanocephalus*. If this were to be true one might expect that *C. m. ouakary* would be a more generalized seed-leaf feeder, eat more quickly and have a shorter passage time to compensate for the less efficient digestive process (Dierenfeld *et al.*, 1992; Herrera & Martinez del Rio, 1998; Lambert, 2002; Milton, 1981, 1984). Unfortunately, the comparative data that will allow this to be tested do not yet fully exist. With 44 families in the diet uacaris at Jaú certainly ate plants from more families than heretofore recorded for a member of the genus *Cacajao* (24 by Ayres, 32 by Boubli, 1997a; 1986a; 34 by Bowler, 2007), but too few studies have been conducted to refute the idea of this as being anything other than a reflection of local plant diversity. In terms of preparing food to enter the gullet, *C. m. ouakary* certainly seems to process food very quickly (Table V-10), but no comparative data has been published for other taxa. Milton (1984) published passage rates for *C. calvus*. The recorded time of five to eight hours was short for a 4kg primate, which Milton related to intestinal anatomy and

the presence if the diet of 'high quality volumetrically concentrated food resources [the effective digestion of which requires] a digestive strategy facilitating the rapid absorption of nutrients without the need for prolonged retention .. [in] the digestive tract'. To date no equivalent studies have been conducted for *C. m. ouakary*, making this an open avenue for future research.

● leaf bases: Both Boubli (1997a: for *C. m. melanocephalus*) and Defler (2004: for *C. m. ouakary* in Colombia) recorded black-faced uacaris eating bromeliad leaf bases. But in neither case is the species or frequency of use reported. Ayres recorded very few instances of leaf-eating for *C. c. calvus,* and bromeliad leaf bases were not among them. Similarly, Bowler (2007) reported that leaves made up only 1.7% of the diet of *C. c. ucayalii,* with all records coming from one species, *Hevea* c.f. *guianensis* (Euphorbiaceae). These were coronets of whole young leaves grouped together before they were separated by shoot elongation (M. Bowler, pers. com.). Bromeliad leaf bases are relatively nutritious (Mondolfi, 1989; Nadkarmi, 1984), providing, for example, the dietary mainstay for Andean bears (*Tremarctos ornatus*: Goldstein, 2004). They are also rich in phosphorus (Winkler & Zotz, 2009). Bromeliads and their individual leaves are both very long lived (Hietz *et al*., 2002), and the meristem is persistent. Thus bromeliads can provide a permanent fall back food that is unaffected by seasonality. For this reason, perhaps, this resource was used at low levels throughout the year by *C. m. ouakary* However, the possibility cannot be discounted that infestation of leaf-base meristems by bromeliad-specific *Metamasius* weevils (Cave *et al*., 2006) may also be providing an additional attraction to *C. m. ouakary* to eat the leaf-bases of *Aechmea mertensii*. An additional possibility was raised by a study of brown mouse lemurs (*Microcebus rufus*:

Atsalis, 2008), a species which eats large amounts of calcium-rich mistletoe berries. Atsalis points out that fruit is often calcium-poor and that the majority of calciumin arthropods is bound in the largely indigestible exoskeleton. However, epiphytes are often richer in calcium because they trap atmospheric dust. Atsalis does not mention bromeliads in this context, but the family is well-known for its ability to use atmospheric dust as a nutrient source (e.g. Malm *et al*., 1998). Thus, it is possible that bromeliad leaf bases might have been eaten as a calcium source, a possibility which future studies could easily test in the laboratory.

● lianas: for other members of the genus *Cacajao* lianas have been shown to provide important fall-back foods. During those parts of the year when overall fruit availability is at a nadir, both *C. c. calvus* (Ayres, 1986a) and *C. m. melanocephalus* (Boubli, 1997a) are reported to increase their consumption fruits from lianas such that liana fruit come to dominate the fruit sector of the diet. At Jaú, in contrast, consumption of liana fruits never dominated the fruit sector of the diet during Phase 3, the period of low fruit availability (Table V-8, Section 5.3.1 and Appendix V-1). During this Phase, fruits from lianas constituted just 5.4% of the diet of golden-backed uacaris at Jaú and even combining all categories, lianas never exceeded 11% of the diet (Table V-9).

Pulp from liana fruits is a seasonally important diet resource for both *C. c. calvus* and *C. m. melanocephalus* (Ayres, 1986a; Boubli, 1997a). However, this was not the case for *C. m. ouakary*, where only three species were used for pulp, and these at very low levels: two Passifloras (2 records each) and one a *Tontalea* (Hippocrataceae: 88 records). These differences may be due to variation between the three study sites in the number of liana species and in their relative densities: during his study of *C. c. ucayalii*, Bowler (2007)

recorded 107 lianas of 13 species from 11 families within his phenology study sample of 1571 trees, lianas and palms (6.8%). While not specifically listing the lianas at his *C. c. calvus* study site, Ayres (1986a) reports that lianas from seven families were present in his 2ha study plot, and that they comprised 39% (N=358) of all plants above 10cm diameter there. In contrast, in the current study, there were just 22 individuals of four species in the 2ha of inventoried igapó (the habitat in which the *C. m. ouakary* at Jaú passed Phase 3, the period of fruit dearth). They constituted just 1.6% of the 1419 trees, lianas and palms in the Jaú study sample.

● pith: Though spongy and of low density, stem pith can be a rich source of energy and quite nutritious (Wizna *et al*., 2008). I have found no published values for pith energetic content for any of the genera that uacaris exploited at Jaú, but published values for sago palm (*Matraxylon sago*) are 2.54 calories/g (Wizna *et al.*, 2008: =0.0105 KJ), and around 4.0 calories/g for lupin pith (*Lupinus*: Pitelka, 1978: =0.0167 KJ). Pith has not been reported previously as a specific diet item for pitheciines, though Robinson (1986) has recorded *Cebus capucinus* eating the pith from the rachis of *Copernia* palms. The energetic values for sago pith are similar to such human foods as aubergine, broccoli, mushroom and squash while those for lupin pith are similar to that of many legume seeds in the human diet (www.positivehealthsteps.com/calories/vegetable).

Cacajao m. ouakary was recorded extracting pith from young stems of *Clusia* c.f. *leprantha*, *Endlicheria chalisa*, *Hevea spruceana*, *Ormosia* sp. and *Pouteria elegans*. As use of pith has not been quantified before as a specific food class for uacaris or bearded sakis, it is presumed that in no previous study was pith eaten sufficiently frequently to be classified separately. Overall *H. spruceana* contributed 62% (54/87) of pith feeding

records, and the relatively high proportion of pith in the diet of Jaú's uacaris probably results from high percentages of *Hevea spruceana* and other favoured pith-producing trees in the igapó study area. Together, four of these contributed 177 (12.5%) of the 1412 trees in the sample plots (as a hemiepiphyte, the fifth pith-providing species, *Clusia* c.f. *leprantha*, was not included in the quantitative surveys). *Hevea* is well-known for forming near-monodominat stands (*seringais*), and in some areas of igapó used by uacaris, approximately one-third of trees were *Hevea*. *Hevea* pith feeding records were concentrated in these areas (36 of 49 records: 73.5%). A contributory factor to the prevalence of pith may well have been the near-simultaneous production across the igapó plant community of new shoots, coincident with the production of new leaves (Parolin *et al*., 2002; Schöngart *et al*., 2002). This phenophase coordination is absent from sites of other published studies of uacari (Ayres, 1986a; Boubli, 1997a; Bowler, 2007), or bearded saki diets (e.g. Pinto, 2008; Veiga, 2006).

What else uacaris eat – animal parts

The capture and ingestion of insects and other arthropods is almost always more difficult to quantify than frugivory or folivory, because of the generally small size of the items, difficulties of observation and lower chances of achieving precise identifications of the species involved (Chivers, 1998). Consumption of arthropods is generally considered to constitute a significant part of the diets only of smaller primates (Redford *et al.,* 1984), while for larger species these energy-rich and protein-dense packages are generally fall-back foods (*sensu* Robbins *et al.*, 2006), used only in seasons of need (e.g. Galetti & Pedroni 1994: *Cebus apella*), or when insects are super-abundant (Isbell, 1998: *Erythrocebus patas*; Srivastava, 1991: *Presbytis entellus*; Tashiro, 2006: *Cercopithecus lhoesti*, *C. mitis*). In line with this general principle, both *C. c. calvus* (Ayres, 1986a) and

C. m. melanocephalus (Boubli, 1997a) are reported to eat more insects during those parts of the year when overall fruit availability is at its nadir, as are *Cacajao*'s close taxonomic neighbours *Ch. satanus* (Frazão, 1991; Veiga, 2006; Veiga & Ferrari, 2006) and *Ch. albinasus* (Pinto, 2008). Direct observation has also recorded arthropods in the diet of *C. c. ucayalii* (Bowler, 2007). In all of these studies, the proportions of insects in the overall diet have been very small (always less than 2% of total annual diet). Fæcal analysis, used as a supplemental technique to establish the diet components of a number of primate species (*Pan troglodytes*: Basabose, 2002; *Rhinopithecus bieti*: Ding & Zhao, 2004; *Gorilla gorilla*: Doran *et al.*, 2002; *Galago* spp.: Harcourt, 1986; *Alouatta seniculus*: Julliot & Sabatier, 1993; Moreno-Black, 1978 summarises earlier studies), generally indicates that insectivory in large primates may be more common than feeding observations alone suggest. Fæcal analysis has never before been used for uacaris, but results of the current study lend support to the notion that insectivory may generally be more common in primates than direct observation indicates, and, specifically, suggests that it may be more common in uacaris than heretofore reported.

In the current study, *C. m. ouakary* was also found to increase observed insect consumption in that part of the year (Phase 3) when fruit availability is lowest. However, while the overall pattern is the same for both other *Cacajao* species and other pitheciines (especially *Chiropotes*), there are some intriguing differences between them: caterpillars, for example, were an item notably absent from the diet of uacaris at Jaú.

As noted above, with the exception of the ingestion of the occasional large *Automeris* sp. (Saturniidae: Helimeucinae) caterpillar, *C. m. ouakary* at Jaú appear to have concentrated on small leaf-mining and leaf-burrowing forms when eating caterpillars; no

records were obtained that parallel those of Ayres (1986a: *C. c. calvus*) and Veiga (2006: *Ch. satanus*), who reported their study species would visit tree canopies specifically to feed on large aggregations of caterpillars. The caterpillars that *C. c. calvus* and *Ch. satanus* ate both appear to have possessed toxic chemicals or irritant hairs, and the primates processed them with considerable care and caution (Ayres, 1986a; Veiga, 2006, respectively). Heavy infestations of young *E. tenuifolia* leaves by Hesperiid caterpillars were ignored by uacaris at Jaú, even as the primates ate the emerging leaves of uninfested conspecifics. My observations of *C. m. ouakary* extracting Tortricid moth larvæ from the leaflets of *Swartzia acuminata* (Section 5.3.7), parallel those of Veiga & Ferrari (2006) who record a similar behaviour for *Ch. satanas,* with individuals extracting notodontid moth larvæ from young, still folded (L. Veiga, pers. comm.), leaves of *Berthollettia excelsa* (Lecythidaceae).

I observed six cases in which abundant lepidopteran larvæ were not eaten by golden-backed uacaris. In three instances larvæ were not touched even when the uacaris were feeding on parts of the very same trees. In five of these six cases, the lepidopteran larvæ involved had strong physical or chemical defences: the black Heliconiinae larvæ feeding on the young leaves of periquitera (*Buchenavia ochrograma*: Combretaceae), were not only spiky (Fig. V-17), but eating a family whose leaves possess nephotoxins (Frone & Pfänder, 2004), and whilst uacaris eat *Buchenavia* leaves (Barnett *et al*., 2005), Heliconiin larvæ are well known for bioconcentrating toxins in their host plants (Hay-Roe & Nation, 2007). Aposomatic Dalceridae larvæ (Fig. V-17) feeding on the leaves of cristo de galo (*Securidaca* sp.: Polygalaceae) can biosynthesize toxins including cyanoglucoscides (Niehuis *et al.,* 2006); these chemicals can kill or severely disable

mammals that ingest even small quantities of them (Roth & Eisner, 1962; Rothschild *et al.*, 1970). The social caterpillars of the saturniid *Arsenura armida* avoided by uacaris are lethally toxic to some vertebrate predators (e.g. chicks of the trogon bird: Costa *et al*., 2003). The uacaris in the current study also avoided Lasiocampidae and Lymantriidae caterpillars. Many of the former are both hairy and toxic, while for the latter, the defence is both long barbed setae which are both irritant and toxic (Deml & Dettner, 1995; Owen, 1980). Together these scattered observations may indicate golden-backed uacaris either ignore or avoid some arthropod species, and that such species are either toxic or noxious. An exception to this is the record of a *C. m. ouakary* feeding on a larval Pyralid or Tortricid moth that lay concealed between two young *Duroia* leaves. Larvæ in some pyralid genera can sequester defensive chemicals from their food plant (e.g. Carrel, 2001), and the genus *Duroia* is notably rich in these (Page *et al*., 1994).

Heliconiinae larvæ

Dalcerid larvæ

***Fig V-17: Noxious Caterpillars Avoided by* Cacajao melanocephalus ouakary**

From this preliminary evidence, golden-backed uacaris appear to be selecting only non-toxic caterpillars even if they are neither especially abundant nor available for extended periods. This strongly contrasts with observations of both Ayres (1986a) on *C. c. calvus*, and Veiga & Ferrari (2006) on *Ch. satanus*. In both instances caterpillars were the focus of bouts of extended foraging that lasted for several days, during which caterpillars

dominated the diet. In the case of *C. c. calvus*, a noctuid caterpillar feeding on young leaves of *Piranhea trifoliata* (Euphorbiaceae) briefly constituted nearly 20% of the total diet. Veiga & Ferrari (2006) reported that over a three day period *Ch. satanus* fed on notodontid caterpillars. These are often well protected chemically (Attygalle *et al.*, 1993), and the authors reported that the microcarnivory occurred in spite of the obvious skin irritation that handling the insects was causing to the hands of the bearded sakis involved.

Larger insects, such as Orthoptera, were occasional items in the *C. m. ouakary* diet at Jaú. Other *Cacajao* species have been recorded eating small insects such as termites, ants and orthoptera (Ayres, 1986a; Boubli, 1997a, Bowler, 2007), as have other pitheciines (Ayres & Nessimian, 1982: *Cacajao* and *Chiropotes*; Harrison-Levine, 2003: *Pithecia*; Heymann & Bartecki, 1990: *Pithecia*; Kinzey & Norconk, 1993: *Chiropotes* and *Pithecia*).

Fæcal analyses for *C. m. ouakary* do not cover all months. It is hard to compare even this preliminary analysis of proportions of insects in uacari fæces with what is known for other pitheciines, because of the lack of comparable data. However, initial data suggest that, as is commonly supposed (e.g. Ayres & Nessimian, 1982; Boubli, 1997a; Bowler, 2007; Pinto, 2008; Veiga & Ferrari, 2006), insectivory is often underestimated in frugivorous primates. Until the collected ant taxa are fully identified, and their behaviour and defence systems understood, it will not be possible to give an informed answer to why, for example, some types of apparently free-ranging ants are included in the uacari diet, while other species symbiotically associated with plants act to deter uacaris from eating their botanical associate (e.g. some individuals of *Macrolobium acaciifolium*).

Opportunistic foraging by travelling uacaris on fortuitously encountered invertebrates, observed in the current study for *C. m. ouakary*, has also been reported for *C. m. melanocephalus* (Boulbi, 1997a), and for *C. c. ucayalii* (Bowler, 2007). Individuals of these species grabbed at passing Lepidoptera and Orthoptera and plucked spiders from the substrate (Bowler, 2007; Boubli, 1997a). As with *C. m. ouakary*, Veiga & Ferrari (2006) reported *Ch. satanus* plucking insects from spiders' webs and searching the dry pyxidia of dehisced *Eschweilera* for edible arthropods.

However, several of the invertebrates recorded in the current study have not been recorded for other uacaris (nor, for other pitheciines). These include the larvæ of *Polybia* wasps (Polistidae), fulgorids, and whip-scorpions. *Polistes* (a genus closely-related to *Polybia*) have been recorded in the diet of *Cebus* (Fragaszy *et al.*, 2004), but not *Polybia*. I have not found any published record of primates eating fulgorids *per se*, though Ayres (1986a) records a young female *C. c. calvus* eating homopteran nymphs (family unidentified). Predation (of any kind) on whip-scorpions is an exceptionally rare event (Rayor & Taylor, 2006; L.S. Rayor, pers. comm.), and the single observation in 2005 was probably the result of an accidental encounter, rather than active searching.

Ants were recorded as part of the uacari diet, both by observation (Appendix V-3) and from fæcal analysis (Section 5.3.10). Ants were a minor diet item in Ayres' (1986a) stomach contents analysis of a *C. m. ouakary* and of a *C. c. calvus*. Ants were recorded for *Ch. satanus* by Veiga & Ferrari (2006) where, as in the current study, both alates and workers were taken. Collectively ants, caterpillar, katydids, mantids and termites constituted 1.7% of *C. c. ucayalii* feeding records recorded by Bowler (2007). Bowler

does not record specifics, except the removal of commensal ants from hollow terminal stems of *Couroupita guinanense* (Lecythidaceae), and the catching of flying termites.

The reactions of *C. m. ouakary* to wasps appear inconsistent; while they eat wasps at their nests, they actively avoid these nests when choosing sleeping trees (Section 4.4.5). A similar situation is known for the genus *Cebus* where, though capuchins eat adult and larval wasps, they also avoid wasp nests with sufficient frequency that pairs of rufous-naped wrens (*Campylorhynchus rufinucha*) who nest near wasp nests suffer significantly less predation from white-faced capuchins (*Cebus capucinus*), their major nest predator, than pairs who do not (Joyce, 1993). Reasons for such inconsistency await elucidation.

Janson & Boinski (1992) noted that the larger the cebine, the less the reliance on mobile insect prey and the greater the importance of large, hidden or well-protected insects, such as large beetles, wood-boring larvæ, and larger social hymenoptera, such as wasps. These authors found that, as a result of size-related biomechanical consequences, larger primates, like capuchin monkeys, could affect searches in tough substrates that need force to open (such as bark, dead wood, carton and epiphyte root masses). By contrast, smaller species, such as squirrel monkeys, lacking such force, obtained most of their insect prey from exposed surfaces or by accessing those concealed in localities that do not require much force to open (e.g. curled leaves, leaf bases). Despite a size which is similar to capuchins and having jaws which are probably far more powerful than a squirrel monkey's, uacaris appear to practise a form of insectivory that is far closer to that of *Saimiri* than to *Cebus.* This may be because, in primates, arthropods are generally processed with the posterior dentition, and the near cuspless molars of *Cacajao* (Hershkovitz, 1987a; Kinzey, 1994) are not suitable for masticating the thick-but-brittle

chitinous coverings of larger insects. It may be significant that the only large insects that uacaris appeared to eat were wood-boring beetle larvæ whose habitat, a tough outer covering surrounding a soft interior entity, is not dissimilar to a hard-husked seed, but whose body (like a seed itself) is soft and pulpy.

● microcarnivory - larvæ within dead wood: larvæ of wood boring beetles were not retrieved directly, but I did encounter dead wood bearing, across the central frass-filled lumen, characteristic uacari dental impressions. In all nine cases, the diameter of the tunnel was never less than 0.5cm (max. 1.4cm), indicating the presence of substantial larval animals (probably of Cerambycid beetles). Though they are rich in energy (Dufour, 1987), the specific use by uacaris of larvæ of xylophageous coleoptera as food items has been considered neither by Ayres (1986a), Boubli (1997a), or Bowler (2007), nor by Aquino & Encarnatión (1999) in their various analyses of uacari diets. Consumption of beetle larvæ has been widely reported for other Neotropical primates (e.g. Mittermeier *et al*., 1983; Veiga & Ferrari, 2006: *Chiropotes*), but not deep wood tunneling forms. One of the few primate species to feed on such larvæ is the Aye-aye (*Daubentonia madagascariensis*) which, like the uacaris, is a specialist in structurally defended resources (Erickson, 1994; Sterling, 1994). It may be that other Neotropical species simply cannot access this potentially valuable resource, and only the robust dentition of *Cacajao*, adapted as it is for sclerocarpic foraging, can break open the relatively thick branches inhabited by such large larvæ.

● microcarnivory - larvæ within fruits: Consumption of insects in fruit is often assumed to be passive (e.g. Link, 2003), and indeed it will be with fruit such as figs, where microcarnivory is inevitable. But, in other cases, active choice of infested fruits by

vertebrate consumers, including primates, is possible. Though he did not investigate this, Ayres (1986a) considered that fruits containing insects might be selected positively by *C. c. calvus* over those that lacked insects inside them. Certainly, such active positive selection for infested fruits has been shown for squirrels (Steele *et al*., 1996), and *Peromyscus* mice (Semel & Anderson, 1988), and Rocha *et al*. (1998) provide an example of active selection by *Cebus apella* of insect-infested fruits, even to the extent of investing in tool use to extract them. Overall, and despite a key review by Redford *et al.* (1984), this aspect of the primate diet seems to be significantly under-researched and clearly in need of further study.

Infested fruits may be nutritionally more rewarding, since larvæ synthesize proteins and fat (Valburg, 1992). Such fruits may also be higher in vitamins (Semel & Anderson, 1988; Steele *et al.*, 1996). Diet fruits infested by insect larvæ were retrieved for 25 of those species eaten by golden-backed uacaris at Jaú. Levels of infestation similar to those reported in the current study (up to 37% of entire fruit wet weight, and up to 73% of seed weight) were found for *C. c. calvus* diet items by Ayres (1986a, 1989), who noted that many immature fruits become heavily infested with coleopteran larvæ and cited as an example *Licania parviflora* (Chrysobalenaceae) where he found 36.3% of 80 young fruit (N=29) contained larval beetles. The dietary importance of such insects has been considered for a number of authors, even if they have not quantified it (e.g. *Callicebus torquatus* and *Lagothrix lagothricha*, Milton & Nessimian, 1984; *C. c. calvus, C. melanocephalus, Ch. albinasus* and *Ch. satanus*, Ayres, 1988).

In not all species where insects were present, were the seeds eaten. For the igapó legume *Parkia discolor*, and for *Inga obidensis* and *I. rhynchocalyx* (both trees from terra

firme), uacaris left infested seeds in the pod, while uninfested seeds in the same pod were extracted and eaten. This may be because, in some instances, infesting larvæ produce chemical repellents or seed chemistry changes in an attempt to kill the invading animal (Janzen, 1977; Sallabanks & Courtney, 1992). Thus the infested seeds many have been toxic, while the uninfested ones were not.

● microcarnivory - small vertebrates: In general, Pitheciines seem to gain their animal protein from arthropods (e.g. Ayres & Nessimian, 1982; Veiga & Ferrari, 2006), and records of small vertebrate predation are rare, and apparently the product of opportunity and curiosity. This contrasts with the similar sized *Cebus albifrons* and *Ce. apella* where small vertebrates (including other mammals) are often a significant component of the diet (e.g. Fedigan, 1990; Resende *et al.*, 2003; Sampaio & Ferrari, 2005). However, a male *C. c. ucayalii* was observed by Bowler (2007) holding a small, partially eaten lizard, and during the 2005 preliminary study I observed an adult female uacari grab and eat a tree frog (prob. *Hyla boans*) as, disturbed by the monkey's foraging, the amphibian moved from concealment beneath an epiphytic bromeliad, though during the current study uacaris were not seen to prey on vertebrates.

5.4.6 Diet and Dentition

As noted in Chapter 1 (and Fig. I-2), uacari dentition is highly specialized for a diet of immature seeds extracted from hard-husked fruits. Yet, in the total diet over 30% of the items were not immature seeds, and in Phase 3 immature seeds constituted just 10% of the diet, with leaves comprising 50% of the recorded items. This apparent discrepancy may be resolved by the observations of Rosenberger (1992), who pointed out that dental morphology most closely reflects the physical forces needed to overcome whichever

class of diet items represent the greatest bio-mechanical challenge. This approach has been used by Atsalis (2008) to explain otherwise anomalous features in the dentition of species of mouse lemur (*Microcebus*). In the case of uacaris, the greatest challenge, clearly, is presented by the hard-husked fruit.

5.5 Summary

In conclusion, the diet breadth of *C. m. ouakary* is comparable with that of other members of the genus. Like them, *C. m. ouakary* is a species whose diet is dominated by immature seeds. However, unlike other uacaris, the *C. m. ouakary* diet in Jaú is supplemented by a large number of other non-seed items. This may be a response to the highly fluctuating levels of availability of dietary resources across the year, which is itself a consequence of the highly synchorized phenologies of the igapó plant community. Resource availability at Jaú may be divided into three phases. Golden-backed uacaris at Jaú have a diet in which immature seeds and young leaves each dominate at one particular phase. Unlike other uacari species, golden-backed uacaris appear to make distinct seasonal migrations between habitats, when in the third phase, there appears to be neither sufficient seed nor new leaf resources to support uacaris in igapó and they move to terra firme, where they again eat seeds. This demonstrates heretofore unrecognized flexibilities in habitat use and diet item exploitation by uacaris, a group of primates previously considered to be extreme dietary and habitat specialists. However, the diet is dominated by five plant species, various parts of which are used at different times of the year. This predominance of a small resource base in the diet, gives cause for conservation concern as it may suggest ecological vulnerability underpinning the apparent flexibility of resource use. In addition, the plain fact that igapó apparently cannot support uacaris

year-round is cause for conservation concern since, though it demonstrates ecological flexibility, it also indicates that populations at Jaú may well require contiguous areas of two undisturbed forest types. This may limit areas able to viably sustain these uacari populations.

- Uacaris at Jaú were recorded eating 189 different items in 17 categories from 136 taxa in 87 genera from 44 plant families**.**
- Overall, the diet consisted of 68% seeds, 11% whole fruit-pulp-arils, 10% leaves, 8% flowers and 3% arthropods
- While immature seeds dominated the diet of uacaris at Jaú, flowers and young leaves were seasonally important.
- Arthropods from seven orders were eaten. They contributed 3% of the feeding records. This figure may be augmented by larvæ inside seeds, but their contribution to the diet could not be quantified**.**
- Uacari diet at Jaú varied significantly between Phases of resource availability, being dominated by immature seeds in Phases 1 and 2, and by young leaves in Phase 3.
- The most important dietary species (by number of feeding records) were *Micropholis venusta* (Sapotaceae), *Eschweilera tenuifolia* (Lecythidaceae), *Buchenavia ochrograma* (Combretaceae), *Pouteria elegans* (Sapotaceae) and *Swartzia acuminata* (Fabaceae: Papilionoidae), and the most important families were Fabaceae (19 species), Sapotaceae (19 species), Lecythidaceae (10 species).

- The top ten ranked plant species comprised 58.9% of feeding records, and 20 species (14.7% of identified taxa) were eaten for more than one anatomical part.
- Eleven species were eaten throughout the year. Six (*Buchenavia ochrograma*, *Eschweilera tenuifolia*, *Hevea spruceana*, *Hydrochorea marginata*, *Pouteria elegans* and *Swartzia acuminata*) comprise 32.7% all feeding records and may be considered key resources.
- Of eaten plant taxa, 70 (51.1%) were canopy trees, this included all major species contributing to the uacari diet.
- Uacaris at Jaú displayed considerable subtlety in opening fruits, in selecting portions to be eaten and in avoiding plant defences. Much of that is attributable to dental dexterity.

CHAPTER 6

UACARI FEEDING STRATEGIES

They're living on nuts and berries
They say animals don't worry
They're living on nuts and berries

Talking Heads *Animals* from *Fear of Music*

6.1 Introduction

6.1.1 Foraging and Seasonality

Food availability may vary in time in several ways, including volume, quality and spatial distribution (e.g. Chetry & Mohnot, 2001; Gillespie & Chapman, 2001; González-Zamora *et al*., 2009; van Schaik, 1983; van Schaik & van Hoof, 1983). The energy expended in obtaining food items (travel costs) has been emphasized as a factor which strongly influences which foraging strategy a species adopts (Chapman & Chapman, 2000a,b; Suarez, 2006; Williamson & Dunbar, 1999). However, this must be balanced against other aspects impacting the daily energy budget, including quotidian factors such as avoiding thermal stress (e.g. Stelman *et al*., 2006: *Papio cynocephalus*), ensuring access to water (e.g. Campos & Fedigan, 2009: *Cebus capucinus*), minimizing costs of lactation or pregnancy (e.g. Lappan, 2009b: *Symphalangus syndactylus*), and coping with the costs of group living (e.g. Dias & Strier, 2002: *Brachyteles hypoxanthus*; Teichroeb *et al.*, 2003: *Colobus vellerosus*). There are also occasional, but important, impacts such as finding a mate and defending territory (e.g. Kraus *et al*., 2008: *Microcebus murinus*; Wallace, 2008b: *Ateles chamek*), and avoiding predators (e.g. Ferrari, 2009; Link & Di Fiore, 2009; McGraw & Zuberbühler, 2008). Furthermore, when attempting to meet daily energy requirements and match them against this set of influences, the predictability of exploitable resources must also be considered, as must their rates of depletion and the

possibility that, when visited, a resource may no longer be available in quantities that would repay the energy expended in procuring them (González-Zamora *et al*., 2009: *Ateles geoffroyi*; Patel, 2006: *Propithecus candidus*; Vasudev *et al*., 2008: *Semnopithecus entellus*). An additional variable is that different foods have different bulks, digestibilities and nutrient profiles, and so release energy and nutrients in different ways and at different speeds (Brand, 1978; Cypher *et al*., 2005). Together this suite of variables provides opportunities for a wide variety of social, behavioural and physiological solutions, and the combination of these in primates is great (Dunbar, 1996).

In the broadest sense, the four possible behavioural responses of mammals to seasonal variations in food availability are to change diet proportions, habitat, social structure, and/or time budget (including hibernation and cathemerality). All of these responses to seasonal changes in food availability have been recorded in primates, with the reported combinations falling into seven broad categories:

1) dietary shifts to other resource types (for primate species whose total annual diet is dominated by fruit this means moving to a diet richer in leaves and arthropods: e.g. Blanchard & Crompton (2009: *Indri indri, Propithecus diadema*), Buzzard (2006a: *Cercopithecus* spp.), Norscia *et al*. (2006: *Propithecus verreauxi*), Tecot (2007: *Eulemur rubriventer*):

2) continuing to exploit the same resource type, but switching to previously sub-optimal species (for example, exploiting fruits of species previously ignored because, compared to resources on other contemporaneously available plants, crop sizes are, in some combination, smaller, travel time between patches is greater and patch

depletion rates more rapid: e.g. Phillips (1995: *Cebus capucinus*), Strier (1989: *Brachyteles arachnoides*) Wallace (2008b,c: *Ateles chamek*), White & Wrangham (1988: *Pan paniscus* and *P. troglodytes*):

3) altering home range size (a cause-consequence of the shifts enumerated in 1 and/or 2): e.g. Curtis & Zaramody (1998: *Eulemur mongoz*), Fan *et al.* (2008: *Nomascus concolor jingdongensis*), Lloyd *et al*. (2008: *Cercocebus sanjei*), Ren *et al.* (2009: *Rhinopithecus bieti*), Savini *et al*. (2008: *Hylobates lar*):

4) foraging in smaller groups (also cause-consequence of 1 and/or 2): e.g. Bartlett (2009: *Hylobates lar*), Mulavwa *et al.* (2008: *Pan paniscus*), Vasey (2006: *Varecia rubra*):

5) increasing the amount of time spent foraging: e.g. Blanchard & Crompton (2009*: Indri indri, Propithecus diadema*), Stone (2008: *Saimiri sciureus*), Wallace (2008c: *Ateles chamek*), Zhou *et al.* (2007: *Trachypithecus francoisi*):

6) increasing proportion of time spent resting and so reducing energy requirements: e.g. Giroud *et al*. (2008: *Microcebus murinus*), Tarnaud (2006: *Eulemur fulvus*):

7) shifting the time at which feeding occurs (cathermerality): e.g. Fernandez-Duque & Erkert *et al*. (2006: *Aotus azarai*), Curtis (2007: Lemuridae), Curtis *et al*. (2006: *Eulemur mongoz*), Tattersall (2008: primates).

The amount of food available in a patch is a key element in how primates respond to seasonal change (e.g. Irwin, 2007: *Propithecus diadema*; Wallace, 2008a,b). Heuristically, it is helpful to unpack the concept of 'crop size', for it includes not only what is available now, but what can be predicted to be available in the future (e.g. González-Zamora *et al*., 2009; Ramos-Fernández *et al*., 2004; Wallace, 2008a,b, and Wich *et al*., 2002 for concept overview). This latter aspect is a function of the number and size of fruits available at any one time, the ease with which they can be found by a foraging animal, their maturation rates, and the maturational state at which the primate eats the fruit, as well as length of time the plant continues to produce new fruits that will eventually reach the maturational state at which the primate in question exploits them (Ortiz-Martínez *et al*., 2008; Rodrígues de Moraes *et al.*, 2004; Wich *et al*., 2002). In this chapter I consider the responses of golden-backed uacaris to changes in food resource profiles at Jaú. Dividing their annual cycle into three phases is useful for studying phenology patterns (Chapter 3), social behaviour (Chapter 4), and diet (Chapter 5). However, because of the complexities of the aggregated concept for which 'crop size' is a convenient umbrella term (see above), such a three-part system becomes a little too coarse for some of the more subtle considerations undertaken here, and for that reason, I shall also refer to variation between months in this section, as well as continuing to use the phase-based system.

6.1.2 Aims

The social ecology of *C. m. ouakary* and its relationship to resource availability has not been studied before. Aims were therefore, of necessity, broad, as the parameters had yet to be fully defined and refined, and hence precise studies could not be conducted with the

state of knowledge that existed when the field study began. Accordingly, the study had a series of simple aims upon which future studies can build. The aims of this chapter are:

1) To gain data on group size, sub-group size, spacing of individuals within groups and sub-groups. This will be discussed in Section 6.3.2 (Results), and 6.4.3 (Discussion)

2) To see how these aspects varied across seasonal Phases and to relate any observed patterns to inter-phase variation in general food availability and to diet composition. This is discussed in Section 6.4.1

3) To gain data on changes in time budget and relate this to any observable changes in the spacing, and crop size of the resources exploited in the different Phases. This will be discussed in Section 6.4.4

4) To contextualize the new information from the current study on *C. m. ouakary* dietary patterns and habitat use. To test this new information against existing patterns of resource exploitation by Palaeotropical and Neotropical primates, using predictions of Terborgh & van Schaik (1987) and van Schaik & Pfannes (2005) of the responses of a morphologically specialized medium-sized Neotropical primate to periods of severe change in diet resource availability. This will be discussed in Section 6.4.5.

6.2 Methods

Measures of resource availability followed those in Sections 3.4 and 3.5. Data for time budgets, group size and sub-group size, inter-individual spacing and group spread, and feeding groups are given in sections 4.3.2, 4.3.4 and 4.3.7, respectively.

6.3 Results

6.3.1 Habitat Use

Habitat types

Between the terra firme and igapó habitats a marked seasonal shift in habitat use was recorded: between Oct-Jan uacaris were mainly observed in terra firme (Phase 1, Oct-Feb: Table VI-1). No contacts with uacaris were made in Nov 2006. For all other months for which observations were made (Phases 2, Mar-Jun and 3, Jul-Sep: Table VI-1), uacaris were encountered only in igapó. This pattern most probably reflects the phenological patterns of fruit availability considered in Chapter 3, and matches well to the availability of fruit by month and phase across habitats (Fig. VI-1).

In Phase 3 when there is little fruit anywhere (Fig. VI-1), the golden-backed uacaris remain in igapó and eat leaves and pith (sections 5.3.7 and 5.3.8), which are more abundant in igapó than in terra firme due to the community-wide leaf-flush of this flood pulse synchronized habitat (sections 3.4 and 3.6.3).

Table VI-1: Percentage Contact with Uacaris in Igapó and Terra Firme by Month and Phase

Phase	*Phase 1*				***Phase 2***							*Phase 3*			***Phase 1***				*Phase 2*	
Month	Oct 06	Nov 06	Dec 06	Jan 07	Feb 07	Mar 07	Apr 07	May 07	Jun 07	Jul 07	Aug 07	Sep 07	Oct 07	Nov 07	Dec 07	Jan 08	Feb 08	Mar 08	Apr 08
Terra Firme	100	0	42.8	55.6	18.2.	0	0	0	0	--	0	0	--	--	71.4	50	--	0	0
Igapó	0	0	57.2	44.4	81.8.	100	100	100	100	--	100	100	--	--	28.6	50	--	100	100

Note: uacaris were not seen in Nov 2006, though searched for. There were no observations in Jul, Oct, Nov 07 and Feb 08.

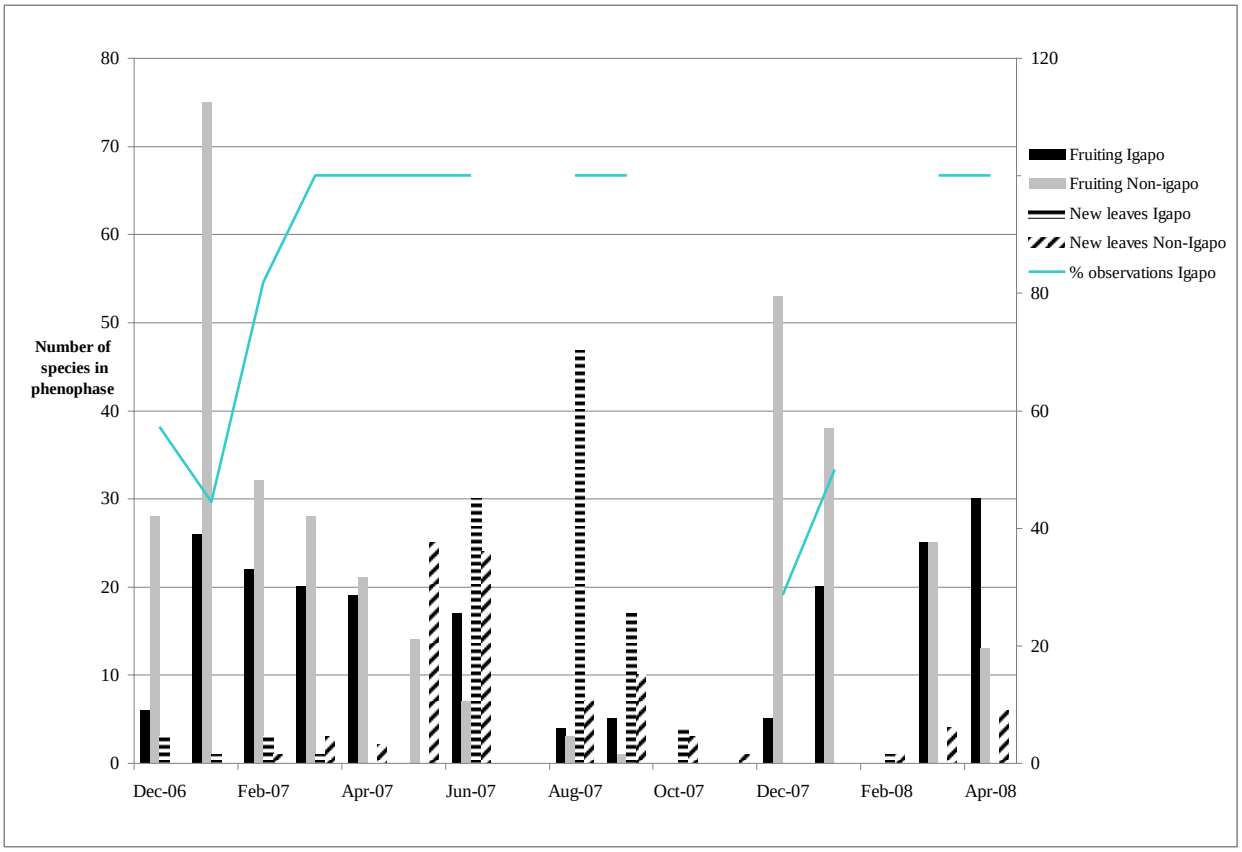


Fig. VI-1: Observed Uacari Presence and Phenology in Habitats by Month, and Phase

6.3.2 Band Size

Band size by habitat

A t-test shows mean band sizes from igapó and terra firme habitats were statistically different (t=10.64, P= <0.005, df=182), when data across phases are combined. The lack of singletons may be an artifact of greater vegetation denisty in the terra firme, which could have made single animals there more difficult to locate.

Table VI-2: Golden-backed Uacari Mean Band Sizes in Terra Firme and Igapó Habitats

Habitat/Data Type	*N*	*Mean Band Size*	*Range of Band Sizes*	*SD*	*No. singletons*
Terra Firme	22	37.5	10-57	16.6	0
Igapó	169	12.3	2-41	8.8	83

Band size by phase

Table VI-3 gives band sizes for arboreally foraging golden-backed uacaris by phase, and Table VI-4 records the results of the pair-wise t-tests to assess if the mean band sizes

recorded in each of the three phases were statistically different from each other. Igapó records from Phase 1 are excluded because of the strong possibility that their small size (5-7 animals) reflected terrestrial foraging activities.

Table VI-3: Mean Band Sizes for Uacaris Arboreally Active in Terra Firme and Igapó

Habitat/Data Type	*N*	*Mean Group Size*	*Range*	*SD*
Phase 1 (terra firme)	22	37.5	10-57	12.79
Phase 2 (igapó)	94	16.06	2-41	9.03
Phase 3 (igapó)	68	6.6	2-13	3.0

Table VI-4: Results of T-tests on Mean Band Sizes

Phases being compared	*t*	*df*	*standard error of difference*	*two tailed value*
Phase 1 vs. Phase 2	8.976	114	2.328,	<0.0001
Phase 2 vs. Phase 3	8.1436	160	1.124	<0.0001
Phase 3 vs. Phase 1	18.604	88	1.661	<0.0001

As can be seen, the differences between the groups in all three comparisons were highly significant. From Nov to Feb (Phase 1) uacaris in terra firme have large band sizes (mean for the Phase is 37.5), with monthly means of between 22 and 39 animals being recorded (Table VI-2). In the period of high fruit resource availability in igapó (Mar-Jun: Phase 2), mean band size is 12.6 and the most commonly seen bands are between 10 and 17 animals. In that period when there are few fruits in either igapó or terra firme (Jul to Oct: Phase 3), uacaris are present in igapó and bands are small: 5-8 animals (monthly means), with a mean band size for the Phase of 6.8.

Factors influencing band size in habitats

The observed band size could be a product of uacari density, caused by inter-individual distances, or by the fission or fusion existing bands of animals. Band size may be influenced by general density of vegetation (Baldellou & Henzi, 1992; van Schaik *et al*., 1983a,b), or by size of feeding trees (Chapman *et al*., 1995), absolute abundance of food

(Robbins *et al*., 1991), and the distances between them (Wrangham *et al*., 1993). The first is widely considered to occur because denser vegetation may offer more concealment for predators, causing primates to increase their proximity as part of a risk-sensitive foraging strategy (Hill & Lee, 1998; Hill & Dunbar, 1998). Feeding tree size as patch size has been widely implicated in primate group size (Snaith & Chapman, 2001), as has travel distance between patches (Chapman & Pavelka, 2005). Accordingly, to investigate the possible reasons for observed differences in band size in different habitats I compared the density of trees both in terms of number of individuals and in terms of mean nearest-neighbour distances for the terra firme and igapó quadrats.

Vegetation Density in Different Habitats: Measurement of the DBH of trees and palms (and excluding lianas) found a mean DBH in terra firme of 60.2cm (N=464) and in igapó of 52.7cm (N=585), with no significant difference between the two habitats (Mann-Whitney U=144554.5, z=1.55124, P= > 0.05, two-tailed test). Mean nearest-neighbour distance of the same trees was 52.5cm in terra firme *vs.* 143cm in igapó, these distances were significantly different (U=133348.5, z=15.1631, P < 0.001, two-tailed test).

Size and Distribution of Feeding Trees in Different Habitats: Distribution of DBH for 183 feeding trees in igapó and from terra firme compared against all trees in study quadrats in both habitats is given in Fig.VI-2. The mean DBH for all feeding trees was 97.5cm. The mean was 84.2cm igapó, and 151.7cm for terra firme (N=147 for igapó, 36 for terra firme). A Mann-Whitney comparison of the DBHs of the feeding trees from each habitat shows they are also significantly different from each other (U=6664.0, z=3.71753, P < 0.001, two-tailed test). Trees of the meam DBH and above (i.e. ≥ 97cm) were not common in either habitat, constituting 12.5% (N=53) of the 465 terra firme trees sampled in this

study, and 8.2% (N=48) of the 584 trees sampled in igapó. As can be seen clearly from the graphic, overall distribution of DBH does not differ greatly between the trees in the two habitats. However, feeding trees are in the larger third of the sample for both habitats. A Mann-Whitney U-test shows that the DBH for the feeding trees alone is significantly different from the DBH of the general sample of trees for both igapó (U=5221.5, z=8.72269, P < 0.001, two-tailed test), and terra firme (U= 26405.0, z = 8.44721, P < 0.001, two-tailed test).

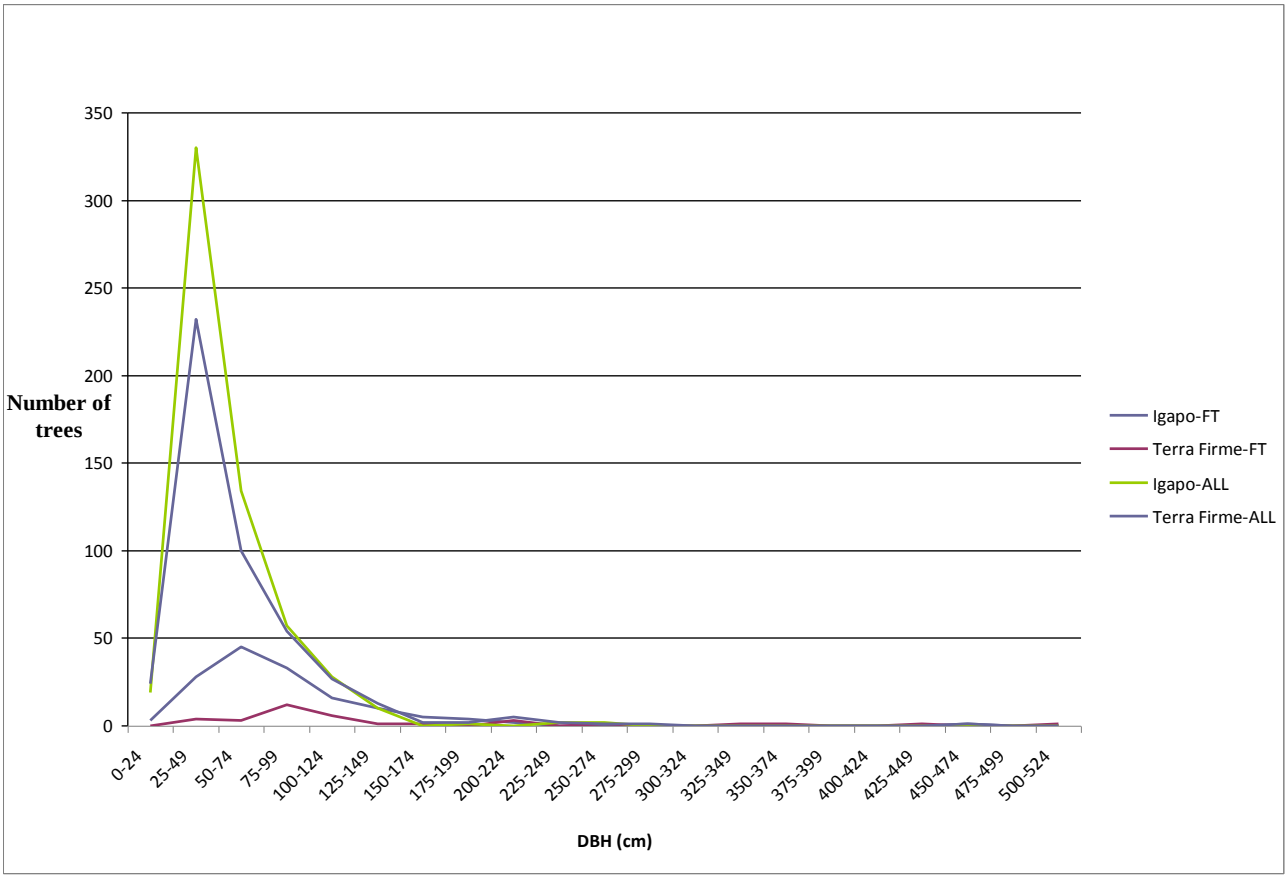


Fig. VI-2: DBH Distributions for Igapó and Terra Firme Feeding Trees and Total Quadrat Samples

6.3.3 Inter-individual Distances

General patterns of spacing

While conducting scan-based samples for time budgets I obtained 908 mean Nearest-Neighbour-Distances (NND) records within travelling bands of uacaris. Table VI-5 gives

mean nearest-neighbour distances whilst uacaris were travelling (including 'moving' and 'moving-foraging') for terra firme and igapó habitats, divided by Phase. Unlike data in Table IV-5 (4.3.4) which compared sexes and age-classes, data here are for all sexes combined (available mother-infant data were excluded to maximize comparability), and focuses on inter-Phase comparisons. Data from uacaris in igapó in Phase 1 are excluded because these animals were foraging terrestrially. I conducted t-tests to ascertain if the differences between the mean values given in Table VI-5 were statistically significant. These were conducted in a pair-wise manner, and the results shown in Table VI-6.

Table VI-5: Nearest Neighbour Distances (NND) for Adult Travelling Uacaris, by Habitat and Phase

Habitat	*No. bands from which data was taken*	*No. NND measurements*	*Mean NND (m)*	*Standard Deviation for mean NND*
Terra Firme Phase 1	10	193	5.27	1.74
Igapó Phase 2	145	502	7.36	4.04
Igapó Phase 3	25	87	9.12	4.60
TOTALS	180	908	7.25	3.5

Table VI-6: Pairwise Statistical Comparisons (T-tests) on Data in Table VI-5

Phases being compared	*t*	*df*	*two tailed P*
Igapó Phase 2 vs. Terra Firme Phase 1	7.0295	693	<0.0001
Igapó Phase 3 vs. Terra Firme Phase 1	10.24	178	<0.0001
Igapó Phase 2 vs. Igapó Phase 3	3.67	587	0.0003

T-test results showed highly significant differences between all three pair-wise comparisons. NNDs are highest in Phase 3 igapó, lowest in Phase 1 terra firme and intermediate in Phase 2 igapó.

Band spread

Contact with travelling golden-backed uacaris occurred on 262 occasions. Band spread (that is, the total distance across multiple sub-units) was not recorded for 40 of these. In 79 cases contact was with a solitary animal. On a further four occasions, the observed

animal was a lone female carrying a dependant infant. Table VI-7 gives band spreads of detectable uacaris in the remaining 149 events, where 2 or more adult individuals of *C. m. ouakary* were observed travelling together. Uacari bands are often quite diffuse with a mean band spread of 207.4 m (N=149), 31.5% of bands spread between 100-200m and 32.9% spread over more than 200m.

Table VI-7: Spread of Uacari Bands in Igapó (m)

Band Spread (m)	***No. Animals***					***Total No. Bands Observed***	***% of Total Observed***
	2-5	***6-15***	***16-25***	***26-40***	***41+***		
To 25m	*11*	*0*	*0*	*0*	*0*	11	7.4
26-50m	*26*	*2*	*0*	*0*	*0*	28	18.8
51-100m	*10*	*2*	*6*	*0*	*0*	18	12.1
101-200m	*3*	*34*	*6*	*4*	*0*	47	31.5
201-275m*	*0*	*23*	*12*	*9*	*1*	45	30.2
TOTALS	50	61	24	13	1	149	100

* this was the limit of reliable visibility in the igapó habitat (Section 4.2.4, Table IV-6)

I also obtained measures of the distance between bands of foraging or moving uacaris, using the 25m separation rule of Symington (1987a,b) to delineate separate sub-groups (foraging units) within a group. Because of vegetation density, these were obtained only from uacari bands in igapó. The mean of 99 measures made from 56 separate daily contacts was 116.6m between such sub-groups (Table VI-7).

6.3.4 Foraging, Party Size and Use of Fruiting Trees

Foraging party size

In single feeding patches, no feeding aggregations of more than five animals were ever observed in any phase. Table VI-8 shows the number of single and multiple feeding records in the same feeding patch (the same tree canopy, or touching crowns of two or more adjacent trees) for adults and weaned sub-adults from 292 feeding records in Phase 2. Of these, 64 (21.9%) were of more than one animal, while 78.1% of records (N=228) were single individual foraging alone for the entire duration of an in-patch feeding bout.

Table VI-8: No. of Uacaris Foraging Simultaneously in Same Food Patch

	No. Uacaris				
	1	***2***	***3***	***4***	***5***
No. Observations	*228*	*38*	*19*	*5*	*2*
% of Total Feeding Observations (N=292)	*78.1*	*13*	*6.5*	*1.7*	*0.7*

Duration of feeding bouts:
Fig. VI-3 shows the frequency of different foraging bout lengths in a single food patch (crown of an individual canopy, or in the touching crowns of adjacent trees) by individual uacaris. The data come from 1597 scans of paused feeding activity, and are organized in 30 second increments. Data are from all phases combined. Golden-backed uacaris do not generally forage for long in any one canopy: 77% (N=1230) of the feeding bouts were of 180 seconds duration or less, and mean foraging bout length in a feeding tree canopy is 148.02 seconds (SD 108.28).

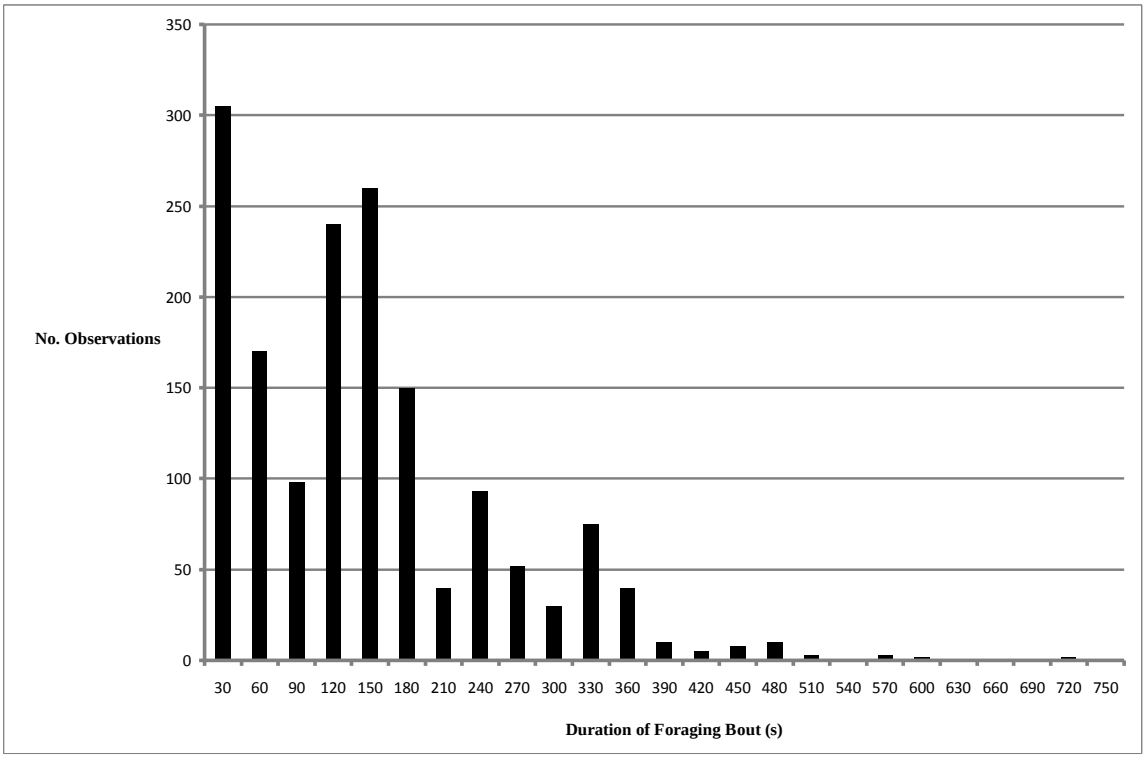


Fig. VI-3: Duration of Golden-backed Uacari Foraging Bouts

6.4 Discussion

6.4.1 Habitat Use

Habitat preferences by uacaris at Jaú

Uacaris at Jaú did not use igapó and terra firme forests equally across months and phases. When flooded and non-flooded forest types are compared (Fig. VI-1), there appears to be an association with the use of forest type and the volume of available fruits for most months. This association does not hold for Phase 3, as during the months of Jul-Sep neither terra firme forest nor igapó significant volumes of fruit (Fig. VI-1). In Phase 3, the *C. m. ouakary* diet is dominated by new and young leaves (Chapter 5), which are most abundant at this time of the year (Chapter 3). The reason why uacaris stay in the igapó at this time cannot be related to size of canopies offering new leaves, since trees in igapó and terra firme forests do not differ significantly in size (sections 6.3.1, 6.3.1.2). Instead, this persistence may relate to the contrasting patterns of leaf-flush that exist between the two habitats. In igapó, Phase 3 is the period of near-simultaneous leaf change in this habitat, with the great majority of tree species dropping old leaves then producing new ones in near-synchrony over a single three month period (Maia & Piedade, 2002a,b; Parolin *et al*., 2002; Revilla, 1981). Igapó's intense phenological pulse contrasts greatly with terra firme's situation. Here there is no single peak of trans-community phenological activity (Parolin *et al*., 2002; Van Schaik & Pfannes, 2005), and both individual trees and individual species may drop and replace leaves over several months, and different species may be found in this phenophase in almost all months of the year (Alencar *et al.*, 1979; Pires-O'Brien, 1993). Thus, for the golden-backed uacari, facultative folivory becomes a strategy to minimize the extent of a negative energy budget during this period, since travel time between patches (and hence energy expended in travel) will be minimized. As tree

density in igapó is twice what it is in terra firme (sections 6.3.1, 6.3.2), it may therefore be possible for uacaris both to minimize travelling and to maximize the item-per-unit-time of foraging. This conservation of energetic expenditure may well be important in a milieu when the food being ingested is of high volume and, for a frugivore, of comparatively low digestibility. Combined, these factors might mean that Phase 3 was not one of positive energy balance for the uacaris at Jaú. Under such circumstances, conserving travelling time may be the most easily available option for maintaining body condition. For golden-backed uacaris the result of this energy-conservation is the foraging pattern displayed at Jaú, feeding on the most easily-accessible item in its most abundant locale. This pattern is consistent with the kind of behaviours that would result if golden-backed uacaris were tracking fruit availability in igapó and terra firme habitats, and occupying the one that maximizes their chances of finding fruit. This kind of trans-habitat resource tracking has been reported for a number of primate species (e.g. Buzzard, 2006b: *Ceropithecus campbelli, C. petaurista,* and *C. diana*; Li *et al.,* 2000: *Rhinopithecus roxellana*; Meyers & Wright, 1993: *Propithecus* spp.; Wallace, 2006, 2008a,b,c: *Ateles chamek*. Brockman & van Schaik, 2005 and Hemingway & Bynum, 2005 provide topic reviews).

Habitat switching

Cacajao m. ouakary at Jaú appear to make seasonal use of different habitats. This kind of pattern has been widely reported for primates (e.g. Branch, 1983 for Black-and-white tassel-ear marmoset *Callithrix humeralifer,* Dusky titi *Callicebus moloch, Saimiri sciureus, Cebus albifrons, Ce. apella, Pithecia monarchus, Ch. albinasus, Alouatta belzebul, A. belzebuth, Ateles paniscus*; Overdorff, 1996 for red-bellied lemur, *Eulemur rubriventer* and red-fronted lemurs, *E. fulvus rufus*; Li *et al.,* 2000 for snub-nosed monkey, *Rhinopithecus roxellana*; Wallace, 2006 for black spider monkey, *Ateles*

chamek; Gómez-Posada *et al*., 2007 for red howlers, *Alouatta seniculus*). As with with *C. m. ouakary* in the current study (Chapter 5), movement between different vegetation types by primates is often related to seasonal fluctuations in food resource availability (Hemingway & Bynum, 2005).

In other uacari taxa, such movements have been recorded, but there is variation in the reasons that underpin why they are made. For *C. c. ucayalii,* which occurs all along the northern part of Peru's Río Ucayali, populations in different areas have variously been recorded as moving seasonally between terra firme and flooded forest, or remaining entirely in either one of the two (Aquino, 1998; Bodmer *et al*., 1998; Heymann, 1990; Leonard & Bennett, 1995). The population studied by Bowler (2007) at Lago Preto showed seasonal preferences for terra firme, *várzea* (white-water seasonally flooded forest), and *Mauritia flexuosa* dominated palm swamps. This shows a great flexibility in the habitat requirement patterns of *C. c. ucayalii*. By contrast, the group of *C. c. calvus* studied by Ayres (1986a) inhabited a large fluvial island, with long fingers of briefly-inundated forest on levées, surrounded by forests that have up to 9 months of inundation. There was no palm swamp and no access to terra firme. Ayres' (1986a) study was the first to be conducted on the genus and, unaware of the flexibility of other members of the genus, he sought to explain the fact that *Cacajao* is restricted to the north-western Amazon basin with the proposal that terra firme – occupied by the ecologically similar *Chiropotes* – had acted as an effective barrier to the dispersal of the genus *Cacajao* from its centre of origin on the shores of the Holocene lake that occupied much of the region. As data from the current study and those on *C. c. ucayalii* are revealing, *C. c. calvus* appears to be rather unusual in its exclusive use of flooded forest.

6.4.2 Inter-individual Distances

The mean nearest-neighbour distance for golden-backed uacaris at Jaú (7.25m) exceeds that for other group-living large non-specialist primate species where nearest-neighbour distance has been reported (Table IV-15).

Dispersal of resources plays a large part in determining inter-individual distances (Di Fiore & Campbell, 2007; Fragaszy *et al*., 2004; Jack, 2007). *Cebus* and *Saimiri* are both generalists with diets that have higher proportions of invertebrates and fruit pulp (Fragaszy *et al*., 2004; Terborgh, 1983) than that of primarily folivorous *Alouatta* (Martins, 2008; Pavelka & Knopf, 2004). Therefore, given the very different diets in the four genera, I consider the most likely explanation for the differences in group spread distances between *Cacajao, Alouatta, Cebus* and *Saimiri* to be related to the concentrated nature of resources the latter three species exploit, and the small patch sizes in which such resources occur (Arrowood *et al*., 2003; de Moraes *et al.*, 1998; Norconk & Kinzey, 1994). While golden-backed uacaris at Jaú do feed in pairs or small units, it was most common for them to be seen feeding alone in a single patch (either the canopy of a single tree or of one or more contiguous ones: Table VI-8). Golden-backed uacaris therefore appear to behave as though they are proximity adverse. This is unusual in Neotropical frugivorous primates where it is common for multiple animals to occupy the canopy of a tree in which they are feeding simultaneously (e.g. Boubli, 1997a; Bowler 2007; de Moreas *et al.*, 1998; Robinson, 1986; van Roosmalen, 1985b; Veiga, 2006). The behaviour maybe related to the observation of Schaefer *et al.* (2002) that the calorific content of fruits and seeds increases with their maturity. Thus the immature seeds ingested by uacaris may yield relatively low energetic returns, even though the canopy of a given tree may be numerically rich in fruits. The available energy might be further reduced by

presence of tannins which combine with proteins and reduce their digestability, and hence the energetic yield of a food item (e.g. Mitaru *et al*., 1984; Nyachoti *et al.,* 1997), and toxins which require energy investment to detoxify (Chung-MacCoubrey *et al*., 1997; Schoonhoven & Meerman, 1978; Weins *et al*., 2006).

Individual avoidance and large nearest neighbour distances may minimize competition and the loss of time and energy involved in defending a low quality resource.

6.4.3 Band Size

Table VI-2 (Section 6.3.2) shows a range and variety of band sizes for Jaú's golden-backed uacaris. Such variation is common in uacari field studies (Defler, 1999 for *C. m. ouakary*; Ayres, 1986a; Bowler, 2007 and Knogge *et al.,* 2006 for *C. calvus*), and is in line with the fission-fusion sociality of the genus *Cacajao* (Defler, 1999), a system which is shared by number of species that exploit forests in which resources fluctuate temporally and spatially and in which patch size may be unpredictable (Aureli *et al*., 2008; Lehmann *et al*., 2007). It should be noted that, as Curtis & Zaramody (1998) have shown with their study of seasonal diet and group size variation in *Eulemur mongoz,* it is not change *per se* that primates respond to, nor types of food available, but whether the available foods provide sufficient energy to meet daily needs (Hemingway & Bynum, 2005).

Observed changes in *C. m. ouakary* band size may be explained as a response to variation in resource availability, in line with both the foraging competition minimization and travel minimization models proposed for fission-fusion sociality (Symington, 1987a,b; Chapman *et al.,* 1995). Sightings of golden-backed uacaris in terra firme were few, but were nearly always of large groups (tables VI-2 and 3). In terms of species composition, Jaú's terra firme forests have the high level of species richness typical of the habitat (Chapter 3). Because there are many species, but very few individuals of each, for

a foraging primate the predictability of encountering a fruiting tree of a particular species is low. This will be most pronounced if, as suggested for many primates (e.g. Garber 1989; Garber & Paciulli, 1997; Janson, 1998), foraging does not purely involve memory-based movements, but is based on a Lévy-walk (as Ramos-Fernández *et al.*, 2004 have found for foraging spider monkeys). Even if spatial memory is the predominant guide, then uacaris foraging in terra firme will still face considerable, energetically costly, travelling times between patches (Garber, 1987).

However, unlike other frugivorous primates with fission-fusion foraging (e.g. *Ateles*, *Lagothrix*, *Pan*, and *Varecia*: Chapman *et al.*, 1995; Di Fiore & Campbell, 2007; van Roosmalen, 1985b; Vasey, 2006), where it is common to have more than one conspecific foraging simultaneously in the same canopy, *C. m. ouakary* at Jaú do not seem to forage in close proximity. It is very uncommon for two or more uacaris to forage in a tree simultaneously, only around a fifth of feeding records coming from multiple individuals in the same canopy (Table VI-8, Section 6.3.4). As with inter-individual distances (Section 6.4.2), Schaefer *et al.* (2002)'s observation that calorific value of fruits and seeds are lower when unripe than when mature offer a possible explanation. Thus, when foraging in a canopy of unripe fruits, *C. m. ouakary* may be in a 'field of abundant poverty', a food patch which, despite the numerical abundance of its individual food items, is not a rich source of energy. Even large food patches may therefore be insufficient to support more than one *C. m. ouakary*. Low energetic values per food item might also explain the very rapid foraging bouts (Fig. VI-3: three quarters of the bouts in any one patch were for three mins. or less) and short processing times of food items (the majority < 10 secs: 5.3.4).

Another possibility is that predation risk is higher in terra firme and that uacaris form larger denser bands under such circumstances. This form of facultative response to increased predation pressure has been reported for many primates including from several guenon species (Hill & Lee, 1998), and Sumatran macaques (*Macaca fasicularis*: van Schaik *et al.*, 1983a,b). Though some examples of the reverse are known, with increased predation pressure leading to smaller group sizes (e.g. Stanford, 1995), the general trend is for group size to increase with predation levels up to limits imposed by food competition and cognition (Dunbar, 1996). The benefits of an increase are considered to be increased vigilance and reduced chance of individual predation (Janson & Goldsmith, 1995).

Both rate and risk of predation can have significant impacts on primate grouping behaviour (Hill & Dunbar, 1998). Risk is a function not only of predator density, but of the primates' ability to detect such predators (Stanford, 2002). Vegetation density is a frequently-cited component of this variable (e.g. Cowlishaw, 1997a,b,c; Hill & Lee, 1998; van Schaik *et al.*, 1983a,b). Tree trunk size does not differ between igapó and terra firme, and trees are substantially closer together in igapó than in terra firme (Section 6.3.3.). However, as igapó is flooded to the depth of several metres for most of the year, there is more available understory vegetation in terra firme, and in this an animal could conceal itself (compare images in Fig. II-4). Thus, predators may be more difficult to detect in terra firme than igapó, leading to larger uacari band sizes.

Predation risk is exceedingly difficult to quantify (Di Fiore, 2002; Enstam, 2007; Hill & Weingrill, 2007), but uacaris have been recorded as victims of aerial attacks by harpy eagles (Barnett *et al.*, in press), and there are many records of primates the size of uacaris being attacked by aerial and terrestrial predators (Di Fiore, 2002; Ferrari, 2009). But are

diurnally-active uacaris in terra firme canopy more likely to be the subject of eagle attack than those in the canopy of trees growing in igapó? It seems unlikely, for Brown & Amadon (1989) do not list any large raptor species with igapó as its unique or preferred habitat. Also, in a study of 34 species of raptor in Peru's Manu National Park, Robinson (1994) found only one species that specialized in flooded forests: the slate-coloured hawk (*Leucopternis schistacea*), a medium-sized bird which preys primarily on frogs and small mammals. Raptor species large and powerful enough to take a monkey generally have ranges in excess of 800ha and do not show preferences for any unmodified habitat within this area (Robinson, 1994). In the case of igapó such a lack of habitat specificity by large raptors is all the more likely considering the comparative physical narrowness of this river-margin habitat, and the structural similarity of the canopies of terra firme and igapó (figs. I-4 and I-5).

Forest canopy was identified by Enstam & Isbell (2003) as one of the highest-risk locales for primates in terms of possible predation. But, the lack of preference of potentially predating raptors for igapó or terra firme makes it unlikely that Jaú's golden-backed uacaris are more likely to experience aerial attacks in the canopy of either habitat. However, exposure to predation may vary between the habitats (Hill & Dunbar, 1998; Hill & Lee, 1998; Janson & Goldsmith, 1995). If uacaris foraged in different ways or in different strata in the two adjacent habitats, then (if predation risk were equal in both habitats) they might have a greater risk of being predated in one habitat than another. However, in both habitats, by far the greatest majority of foraging activity by golden-backed uacaris at Jaú had been observed to take place in the upper strata of the canopy. It is possible, but unlikely, that canopy architecture of terra firme and igapó trees differs in

some manner that means visibility of foraging uacaris to aerial predators is not equal in both habitats. Such factors were considered influential by Ramakrishnan & Coss (2001) in their analysis of branch choice of three Asian primate species. The variables involved, such as leaf size, foliage density, three dimensional arrangement of branches and their leaf-bearing segments and how the animals locate themselves when foraging within a canopy have yet to be measured for uacaris.

Non-avian predators of adult uacari-sized primates include jaguars (*Felis onca*: Felidae) and large snakes (Ferrari *et al*., 2004; Matsuda & Izawa, 2008). While both boa constrictors (*Boa constrictor*: Boidae) and anacondas (*Eunectes murinus*: Boidae) have been recorded at Jaú, only the former regularly forage high in trees (Boback, 2005; Heymann, 1987). There appear to be no comparative data on relative densities of either large snakes or large felids in flooded and terra-firme forests. Jaguar activity in flooded igapó clearly can not be monitored by means such as the paw-marks, fæces and scratch marks commonly used to register their presence indirectly (e.g. Furtado *et al*., 2007; Salom-Pérez *et al.,* 2007). However, since jaguars are generalist predators and track both relative and absolute abundance of prey species within their extensive ranges and exploit those areas where prey is concentrated (Seymour, 1989), one may expect them to follow their prey. Prime jaguar prey species, such as red brocket deer (*Mazama americana*: Cervidae*),* collared peccary (*Tayassu tajacu*: Tayassuidae) and white-lipped peccary (*Tayassu pecari*: Tayassuidae), enter igapó forests only when they are unflooded (Bodmer, 1990), when they feed on the deposited and, subsequently, germinating, seeds of hydrochorous species of igapó trees (Bodmer, 1990). It may therefore be expected that jaguar activity in flooded igapó forests will be low, but increase only when it is unflooded.

Jaguar may therefore be more common and more active in the terra firme, and the uacaris respond to this by reducing their inter-individual distances, resulting in denser bands. This kind of response has been observed when uacaris are directly attacked or hear a potential predator: Barnett *et al*. (in press) report that a unit of 14 adult and adolescent golden-backed uacaris gathered in two adjacent tree crowns immediately after one of their number was taken by a harpy eagle. As may be seen from the data in Table VI-5 (Section 6.3.3), such close proximity in uacaris at Jaú is extremely unusual, and such temporary aggregations are considered a functional response to predator proximity and to function on selfish herd principles (Hamilton, 1971), similar to the post-predation shoaling behaviour of fish (e.g. Krause, 1993). As larger bands of primates have been shown to attract predator attention (Stanford, 1995: *Colobus badius tephrosceles*), such post-predation aggregations of uacaris are considered to be temporary and do not imply that a close nucleated bands might be the best way of avoiding the attention of predators. Indeed, as seen below, uacaris at Jaú appear to forage in small bands when in situations of high predation risk.

During the current study, uacaris were observed to move away from a tayra (*Eira barbara*: Mustelidae) that came within 50m of a group foraging in igapó. As they moved away, the uacaris appeared to be travelling in closer proximity than normal (though this event was off-scan and nearest-neighbour distances were not quantified). Golden-backed uacaris respond to the presence of some predators by grouping closer together and, from evidence summarized above and in Section 4.3.8, they appear to be both generally predator aware and capable of distinguishing between dangerous species and those unlikely to pose a survival threat. Accordingly, the possibility that smaller inter-individual

distances are due to increased perceived predation risk in terra firme cannot be discounted, though I consider it most likely that larger band size is a most often a response to the spatial dispersal profile of food in this habitat.

Predation risk and patch size may also have influenced group size when uacaris engaged in terrestrial foraging. In December 2007 and in January 2008, on six separate occasions over five days, uacaris were seen foraging terrestrially on germinating seeds (Section 5.3.2, p. 234). In addition, other small bands were observed in igapó in Dec, Jan, Feb of Phase 1, and may too have been foraging on germinating seeds. These small patches represented very concentrated resources (figs. V-8 and V-9), which large bands of uacaris would have depleted quickly. Also, a small band could quickly perform a 'resource-raid' without summoning such unwanted attention from jaguars, tayra and other carnivores that seasonally visit unflooded igapó, whereas a large band might have had just such an effect.

6.4.4 Foraging, Party Size and the Use of Fruiting Trees

For *C. m. ouakary*, mean arboreal foraging bout length is less than two-and-a-half mins. (Fig. VI-3). In comparison to other primates, this is remarkably short: Aquino (1988), for example, reported feeding bouts in single canopies lasting between 3 and 35 mins. (180-2100 secs) for *C. c. ucayalii,* and Vanderhoff & Grafton (2009) recorded mean feeding bout lengths of 6.65 mins. for *Saguinus midas* feeding in *Ficus* trees. For *Ateles chamek,* the mean for 1262 data records of time entered *vs.* time left individual feeding resources (trees or palms) was 14.5 mins. (range, 1 min. - 2 hrs. 54 mins.: Robert Wallace, pers. com.). For *C. m. ouakary* at Jaú, three-quarters of feeding tree records were of an individual who foraged alone for the entire duration of its feeding bout. This is probably

due to the large distances between both individuals (Table VI-5), as well as the extent of band spread (Table VI-7), and the large distances between sub-bands.

Other fission-fusion species, such as *Ateles*, commonly forage either together in a fruiting canopy, or enter it in quick succession (e.g. van Roosmalen, 1985b). Yet, even in quite large canopied trees with ample crop volumes (such as *Aldina, Eschweilera* and various Sapotaceae), *C. m. ouakary* almost always foraged alone. The question remains, why, when there appear to be plentiful food resources in an individual canopy or patch, do these uacaris so rarely use the same food patch at the same time, and also so very infrequently follow one another into such locales? The tentative answer may be that the fruit crop may be (perhaps chemically?) more heterogeneous than it appears to the human observer. Consequently, effective crop volume for a selective uacari feeder, perhaps choosing only those fruits it is metabolically optimized to digest, may be less than calculated under the simplistic crop volume estimates given in Chapter 3, and patch depletion therefore occurs more frequently than anticipated. If this were the case then Jaú's golden-backed uacaris would be paralleling the red colobus (*Piliocolobus tephrosceles*) studied by Snaith & Chapman (2005), who found that the animals were far more selective of leaves than previously supposed and resources consequently far less homogeneous, that selection was based on age-related chemical criteria, and thus that each patch (tree crown) had a much lower potential food yield than researchers had previously realized.

The structure of uacari sub-groups (foraging units) may also be involved here. In fission-fusion species like *Ateles paniscus,* sub-groups traverse the canopy in near-single files, following a dominant female who leads them to resources. On arrival at the food

patch, individuals in the troop either forage there simultaneously or in rapid succession (van Roosmalen, 1985b). However, though both golden-backed and Peruvian red uacaris (Bowler, 2007) may proceed in a loose file when moving between feeding locales, when foraging the animals advance on a broad front, widely spread and with no apparent leader. This, plus the physical extent of inter-individual distances, may make it difficult for any animal to move swiftly to a patch another band member has just discovered.

Why uacaris travel so fast, and what motivates the uacari at the front of the foraging troop to move, is not yet known, but the consequence is that, on average, an individual uacari attempting to keep up with the troop's general movement will not have long to exploit a patch before having to move forwards and change locations. As expected mean travel time is a key component in determining how long to remain in a feeding patch (Charnov, 1976), short stays could optimize yield if expected inter-patch travel time was small. This is indeed the case in igapó where the combination of lower species diversity, higher numbers of individuals of the same species (e.g. Fig. III-3) and a shorter community-wide fruiting season (Parolin *et al.*, 2002, 2004b), may mean that inter-patch distances is less than for terra firme (which is the habitat of *Ateles*, *Brachyteles*, *Chiropotes*, *Lagothrix* and the other Neotropical primates in which fission-fusion has been recorded). This combination of factors could promote the comparatively shorter in-patch foraging periods recorded for uacaris.

I was unable to identity reliably or even sex the lead individual in the smallest uacari foraging units I observed (3-5 animals), but I did not gain the impression that the lead animal was always the unit's female-with-baby. Indeed, which animal was at the front of the loose line of advancing uacaris seemed to change frequently. If uacari sub-groups are

not, like *Ateles paniscus*, being led by an experienced female, then encounter rates with food trees may be more random with individuals not heading *per se* for specific trees to feed. This might result in animals using the Lévy walk mechanism reported by Ramos-Fernández *et al.* (2004) for *Ateles geoffroyi*. Under such circumstances, where fruit yields from the next patch encounter may be uncertain, repeat small samplings from within a defined area may be an optimal strategy. Underpinning these currently untested ideas is the assumption that the unripe fruits being sampled, in fact, possess, in ways that are important to the uacari, significant heterogeneity either chemically or physically. This, and the notion of leaderless troops, are both predictions that are testable in the field.

6.4.5 Cacajao melanocephalus ouakary *Seasonal Responses in the Broader Context: testing the model of Terborgh & Van Schaik*

The model, its predictions and C. m. ouakary

Terborgh & Van Schaik (1987) made predictions concerning six aspects of the biology of Neotropical primates living under conditions of seasonal resource constraint. These were: 1) ranging flexibility, 2) diet flexibility and body size, 3) diet flexibility and morphology, 4) diet flexibility and available food types, 5) behavioural flexibility and biogeographical peculiarities, and 6) behavioural flexibility and resource seasonality. These predictions, as augmented by Hemingway & Bynum (2005), are presented below, with annotations on how the known biology of *C. m. ouakary* fits with them.

1) Ranging flexibility, Terborgh & Van Schaik (1987) predict that:

i) ranging patterns will change in environments where the grain size of habitat variation exceeds that of the species home range,

ii) when resources are abundant home ranges will overlap with those of other bands and be non-defended,

iii) habitat use will track resource availability (though competitive interactions and availability of sleeping sites may modify responses).

The data presently available on *C. m. ouakary* (from the current study, and the work of Defler, 2004 and Helder Quieroz and students at Amanã [Barnett *et al*., in press]) provides strong support for iii), equivocal support for i) (at least as far as band size and nearest-neighbour distances change with habitat: though actual distances covered remain to be examined). There are no firm data to support or deny ii) as individuals and bands are not yet unequivocally identifiable.

2) Dietary flexibility and body size, Terborgh & Van Schaik (1987) predict that:

i) during periods of restricted food availability smaller primates will consume items such as animal matter, nectar and sap that are energy-rich and relatively easily digested, while medium-sized and larger species will include less digestible material such as leaves and other vegetable matter.

Cacajao m. ouakary is a medium-sized primate and does eat more leaves and pith during times of restricted food availability. However, the response of the species at Jaú only partly fit the model as the proportions in the diet of both insects and nectar also increased when fruit availability declined.

3) Dietary flexibility and morphology, Terborgh & Van Schaik (1987) predict that:

i) those species whose morphologies are specialized are expected to have narrower diets than those species with less specialized morphologies.

Overall, *C. m. ouakary* does fit this prediction. It is certainly specialized: the morphology of the skull and teeth indicate a diet of seeds derived from hard fruits, seeds (immature and mature) comprise nearly

80% of the annual diet, and two-fifths of the 102 species from which seeds were extracted had hard pericarps. However, at some times of the year the *C. m. ouakary* diet includes food types (such as flowers and leaves) whose procurement and processing it does not possess obvious morphological adaptations to affect. Thus, in this aspect, *C. m. ouakary* does not completely fit the model's predictions.

4) Dietary flexibility and availability of food types, Terborgh & Van Schaik (1987) predict that:

i) species with diets that have a high percentage of items with predictably high abundances over extended periods of time will not have diets that show extensive temporal variation.

Terborgh & Van Schaik (1987) considered frugivores to be eating a particularly reliable food source, because phenological succession in Neotropical forest tree communities makes fruit available in large quantities for extended periods of the year. Since the time required for a fruit to mature is greater than the time for which a fruit is mature, this effect may be even more pronounced for a primate species that exploits unripe fruit and seeds, and such a species could be considered to have a very reliable diet. Consequently, *C. m. ouakary* might be expected to conform very strongly to this prediction, yet they do not. The deviation occurs principally because the initial prediction contained an incorrect assumption about food availability and did not take into account habitats like igapó where community-wide availability of food resources shows such strong temporal pulsing in

availability. For *C. m. ouakary*, leaves constitute a very high percentage of the fallback foods, a factor that relates to the unusual nature of igapó habitat and the highly discontinuous nature of the phenology of its plant community.

5) behavioural flexibility and biogeographical particularities, Terborgh & Van Schaik's (1987) predictions are based on general patterns of resource availability in tropical forests in African, Asian and Neotropical forests, and are that:

i) New World primates will rely more on nectar and insects as fall-back foods than Palaeotropical species

ii) Neotropical species will have lower percentages of young leaves in their diets as fall-back foods than Palaeotropical species

The fit of *C. m. ouakary* responses to those predicted in 5i and ii cannot be estimated since there are no Palaeotropical species that have even an approximately similar ecology to that of the genus *Cacajao*.

6) behavioural flexibility and resource seasonality, Terborgh & Van Schaik (1987) predict

i) fallback food resources to which primates switch should be either stable in availability or more available at such times relative to resources which dominate the annual diet, and which might therefore be considered to be preferred. Such items may include foods otherwise rare in inventories of primate diet items, such as bark and lichens.

Observed *C. m. ouakary* responses fit this prediction, to the extent of including unusual foods such as pith, bromeliad leaf bases and burrowing insects in the diet in Phase 3. In addition, leaves constitute a high percentage of the fallback foods. This relates to the unusual

nature of igapó habitat and the highly pulsed nature of the phenology of its plant community.

How and why C. m. ouakary *does and does not fit the model's predictions:*

Simply because such foods are eaten in times when the 'normal' food sources are not available, does not mean fallback foods are nutritionally impoverished (Norconk & Kinzey, 1993). Instead they may be as nutritious, or nearly so, as 'normal' foods, but have either little or no availability at the time in question, or are masked by the presence of preferred species (Hemingway & Bynum, 2005). Wrangham (1980) distinguished between food that provided sufficient energy and nutrients to maintain body functions and prevent death by starvation ('subsistence diet'), and those foods whose more abundant calories and nutrients allowed for individuals to move beyond mere maintenance and permit investment in growth and reproduction ('growth diet'). Hemingway & Bynum (2005) believe that, in general, fallback foods are more likely to constitute a subsistence rather than growth diet. Given that the cranial morphology of *Cacajao* appears so highly specialized for seed predation (Kinzey, 1992), one might predict the substantial foliage component in the fallback diet means that it forms a subsistence diet. However, as the work of MacLarnon *et al*. (1986) has indicated, the presence of caecal fermentation or some other form of alimentary specialization in *Cacajao* cannot be discounted. So, the possibility is open that the items eaten in Phase 3 may not constitute a subsistence diet and might even be a growth diet.

As defined originally by Schoener (1971), energy-maximizers will increase ranging to meet energy needs, while for time-minimizers a diminution of range and an increase in search time for food within a smaller area may be the initial response to reduction in resource availability. If reduction persists, then switching to other foods may occur. As

noted in sections 6.4.4 and 6.4.5, there are indications that *C. m. ouakary* displays elements of both energy-maximizer and time-minimizer strategies.

Hemingway & Bynum (2005) suggest that switching between alternative dietary resources may occur in several different ways: i) between categories (i.e. moving from fruit to leaves to animal matter depending on the relative abundances of the items, e.g. Hill, 1999: *Macaca fuscata*), ii) within categories (i.e. over time using items in the same diet category offered by different species, e.g. gibbons in central Borneo selecting fruits from a sequentially fruiting series of trees, McConkey *et al.*, 2002: *Hylobates muelleri* x *agilis*), and iii) a reliance on a single food species during periods of scarcity (e.g. use of palm fruits by *Cebus* spp. at Manu, Peruvian Amazonia: Terborgh, 1983). At Jaú, *C. m. ouakary* appears to employ the first strategy, switching between diet item categories as resource Phases change from immature seeds available in developing terra firme fruit (Phase 1), to those in fruits maturing on igapó trees (Phase 2), to a situation where fruit (mature or immature) is nowhere common and the only abundant resource is young leaves in igapó (Phase 3). However, *C. c. calvus* appears to employ the second strategy, as the diet reported by Ayres (1986a) was nearly always dominated by some form of immature seed. Populations of *C. c. ucayalii* studied by Bowler (2007) appear to adopt the third strategy, relying almost completely on pulp of the fruit of the burití palm (*Mauritia flexuosa*) for several months of the year when few other resources are available.

A meta-data analysis of 234 quantitative studies of primate diet was used by Hemingway & Bynum (2005) to search for patterns of response to seasonal resource variation in 119 primate species across various diet specializations. Together the species inhabited environments across a variety of intensities of seasonal change, phenological

patterns and levels of resource availability. From this analysis, it appears that, the response of *C. m. ouakary* to seasonal variation in availability of dietary resources is, among Neotropical species, closest to that of the Atelines, which also switch to new leaves when fruits are not available. The alternation between seed- and leaf-eating, recorded in this study for *C. m. ouakary*, is also common in other phylogenetic lines of primates in which immature seeds are an important dietary constituent (e.g. Indridae in Madagascar, especially *Propithecus*, and Colobinae in Asia and continental Africa, especially *Colobus*, *Presbytis* and *Trachypithecus*).

Habitat shifting does not seem to have been reported with great frequency: Hemingway & Bynum (2005) found only 15 instances for their data base. They delineated three ways in which habitat shifting occurs:

i) commuting into a habitat, visiting briefly to use specific targeted resources,

ii) expanding range to include new habitat,

iii) moving entirely to new habitat, and then later moving back to previous one.

At Jaú golden-backed uacaris appear to deploy all three strategies: using data obtained before the current study, Barnett *et al*. (2005) reported *C. m. ouakary* leave flooded igapó, enter terra firme and travel several km to exploit spatially restricted patches of *Mauritia* palm fruits, before returning to igapó on the same day. This occurred in what the current study identifies as phases 2 and 3, when uacaris were otherwise entirely resident in igapó. It therefore conforms to Hemingway & Bynum's commuting option. Uacaris fit Hemingway & Bynum's second option during Phase 1 when they visit dry igapó immediately adjacent to the terra firme forest to feed on germinating seeds. This oscillating habitat use is consistent with Hemingway & Bynum's form ii.

Form iii of these authors, moving entirely to a new habitat, is something that Jaú *C. m. ouakary* do when moving from the igapó it (predominantly) occupied in Phase 3 to the terra firme it (predominantly) occupies in Phase 1. The extent to which *C. m. ouakary* penetrates terra firme appears to vary with location. At Jaú it is no more than a few hundred yards (Barnett *et al*., 2005), but at Caparú, Colombian Amazonia, *C. m. ouakary* bands are reported to move deep into the terra firme and spend weeks there without visiting igapó (Barnett *et al*., in press; Defler, 1999). *Cacajao m. ouakary* may not be the only primate to make seasonal movements to-and-from igapó. Peres (1994a) reported igapó-living *Cebus albifrons* and *Saimiri sciureus* both seasonally expanded their territories to include terra firme, and Palacios & Rodriguez (2001) study showed Colombian *Alouatta seniculus* moved seasonally between these two adjacent habitats.

6.5 Summary

At Jaú, *C. m. ouakary*

- move between habitats tracking diet resources
- have band sizes which vary in relation to dispersion of diet resources (and possibly predation risk) at each Phase
- forage in widely spread foraging units and bands whose inter-individual distances may reflect high resource dispersion, rapid patch depletion rates and low nutritional content of such patches
- rarely feed close together and never aggregate more than five animals to a feeding patch at the same time

- process food quickly and rarely remain for more than a few minutes in any one feeding patch
- have a series of seasonal responses which accord with theoretical predications, except where such predications did not take into account a habitat with the plant community characteristics of igapó.

CHAPTER 7

THE GOLDEN-BACKED UACARI, PAST, PRESENT AND FUTURE

Your descendants shall gather your fruits.
Virgil

7.1 Summary, What We Now Know and Now Know We Don't Know about *C. m. ouakary*

From the previous three chapters it can be said that *Cacajao m. ouakary* prefers the canopy of primary habitats, where it principally eats immature seeds from emergent and canopy trees, supplementing its diet with flowers and leaves, plus the fruits and seeds of smaller plant species when the need arises. Habitat use is seasonal, alternating between terra firme and igapó, and appears to follow the availability of abundant food resources. Individual uacaris rarely spend long in one feeding patch and infrequently forage together. *Cacajao m. ouakary* spends a lot of time foraging and moving, but very little in resting or social interactions. Aggression and grooming are both rare. Sleeping sites are tall isolated trees with few or no points of contact with neighboring canopies. Within these, golden-backed uacaris sleep in the middle of large branches, most frequently alone. Band sizes vary across the seasons, but bands of 6-15 animals were the most commonly seen (Table IV-5).

Several key elements of *C. m. ouakary* biology remain unresolved, such as why they spend so little time foraging in each patch, and why they are so fast-moving. There is very little quantitative information on day and annual ranges, band composition or band dynamics. Nothing is known of dispersal patterns, and whether one or both sexes disperse. Similarly we do not know if smallest observed social group of 5-6 animals is stable and, if it is, the genetic relationship between the members. The mating system

appears to be multi-male, but clarification is required. The unusual features of their activity budget, particularly the very low social time and high travel time, also need to be explained. These uncertainties, plus the fact that what is currently known has been established from just one site, give ample opportunity for future research. Current research priorities are discussed below.

7.2 The Calculating Cacajao: a model for diet item choice in *Cacajao m. ouakary*

7.2.1 Abundance as a Choice Factor

Though there is clearly some selection (Section 5.3.3), the Ivlev Values are generally not high, and golden-backed uacaris appear to be 'skimmers', feeding only on species which are most abundant at the time. This not only applies to the class of resource (whether fruit, flowers or young leaves), but to species within the classes. Species possessing immature fruit for 3-4 months, but with either small crop volumes, few individuals or both (e.g. *Aldina heterophylla*: Fab.: Pap.; *Maprounea guianensis*: Euphorbiaceae; *Ternstroemia candolleana*: Theaceae) are only eaten when fruits are unavailable from species with more individuals, larger crop volumes or both. Additionally, common, abundantly-fruiting species with extended fruiting periods (e.g. *Eschweilera tenuifolia* fruits for 12-14 weeks) may be ignored or downgraded in rank when briefly-producing species transiently exceed them in crop volume (e.g. *Chaunochiron loranthoides*: Olacaeae; and several sequentially-fruiting Sapotaceae, inc. *Eleoloma glabrescens*, *Micropholis venusta*, *Pouteria cuspidata* and *Pouteria elegans*, all of which fruit for 2-6 weeks: Ferreira & Parolin, 2007; Spironello, 1999).

Uacari diet and habitat use is strongly influenced by the phenology of terra firme and igapó, which are slightly off-set in time and so provide an extended suite of resources for

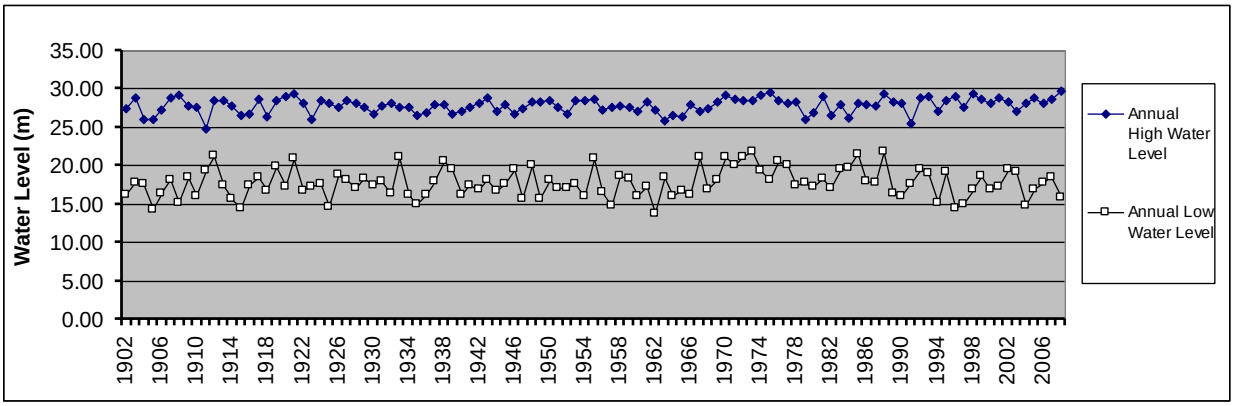
the uacaris. Terra firme has its peak of fruit production in Phase 1 (Nov-Feb), several weeks earlier than igapó where it peaks in Phase 2 (Mar-Jun). Igapó then has a peak of fresh leaf production in Phase 3 (Jul-Oct) when there is little fruit in either habitat. In the period when little fruit was available and before the igapó tree community began its concerted leaf-flush, uacaris sought out species with very small crop sizes that had been available but had been completely ignored before (e.g. *Casearia* sp. and *Laetia corymbulosa*: Flacourtiaceae; *Mouriri guianensis*: Memcylaceae). They also ate the pulp of a toxic-seeded liana, cipó pitomba (*Tontalea* sp.: Hippocrataceae). During the part of Phase 3 when fruit was so rare that it was not recorded by any field survey method, uacaris switched to pith and new leaves.

Thus, *C. m. ouakary* appear to choose to feed on the relatively most abundant species. How this assessment is made remains to be investigated. However, a number of reasons can be advanced why such a strategy might be beneficial when foraging in igapó:

1) Many species of the habitat's numerically dominant trees have biannual peaks in flowering and fruiting. These include such important uacari diet species as *Eschweilera tenuifolia, Mabea nitida, Aldina heterophylla* and *Hevea spruceana* (Leandro Ferreira, pers. com.). As preliminary data in Chapter 3 indicate (and Leandro Ferreira, pers. comm.), populations of such species are fertile in the off-years, but in these years production appears to be very much lower than in peak-years.

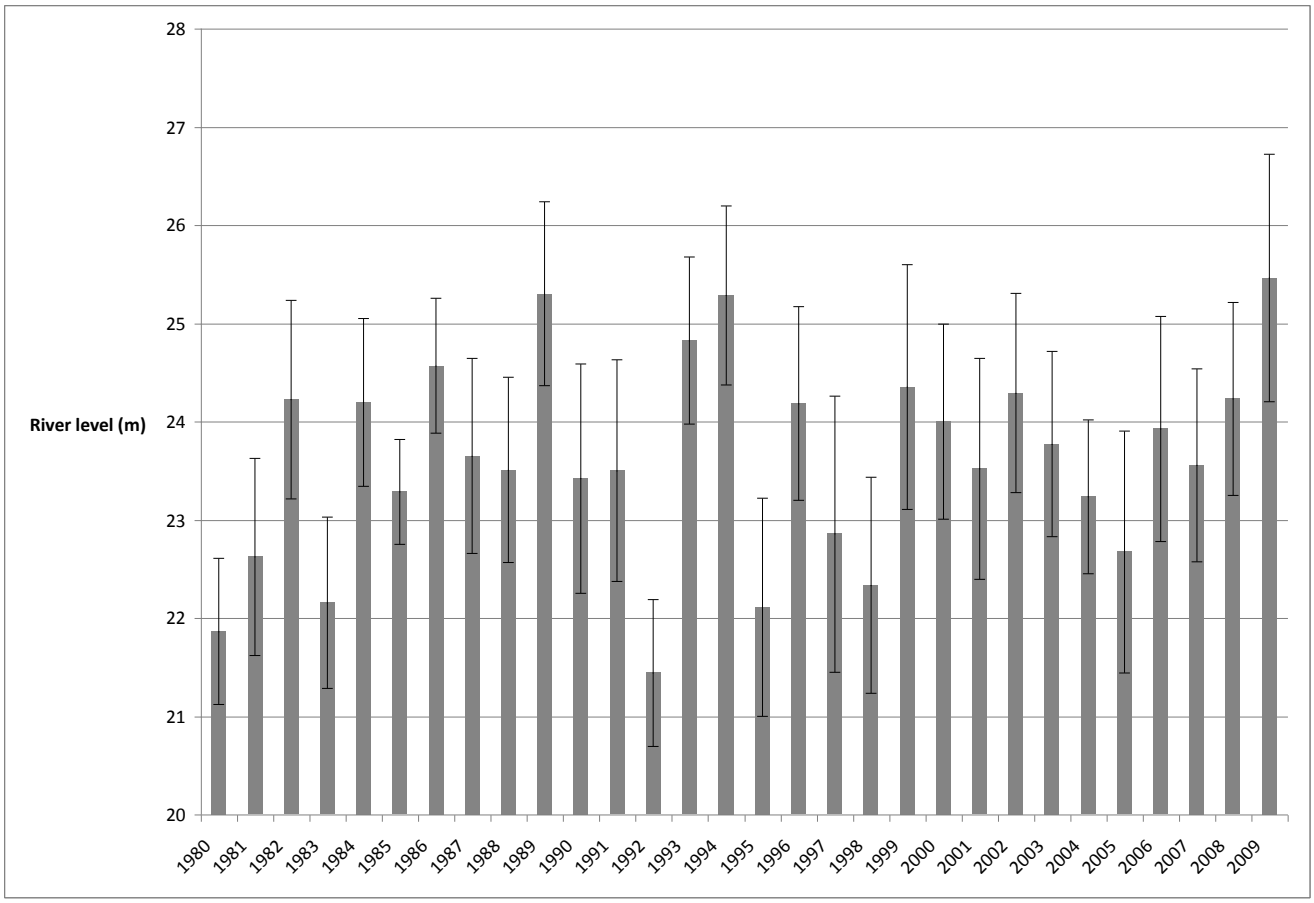
2) The igapó plant community is strongly structured by the tolerance of its component species for inundation duration (Chapter 3; Ferreira & Parolin, 2007). Timing of igapó plant reproduction is largely cued by water levels

(Parolin *et al*., 2002), with the igapó forest fully flooded between Mar and Oct, and the igapó forest floor fully exposed between Nov and Feb. However, there is great inter-annual variation in the annual periods of flooding and low-water (Fig. VII-1), and in both the annual river water volume each year (Fig. VII-2), and on-set their time (Fig. VII-3). In consequence, individual species might be cued to fruit earlier or later depending of the duration and intensity of flood and dry conditions they experienced. Droughts provoke many species to abort or reduce flowering, fruiting and leaf flush (Parolin et al., 2010).



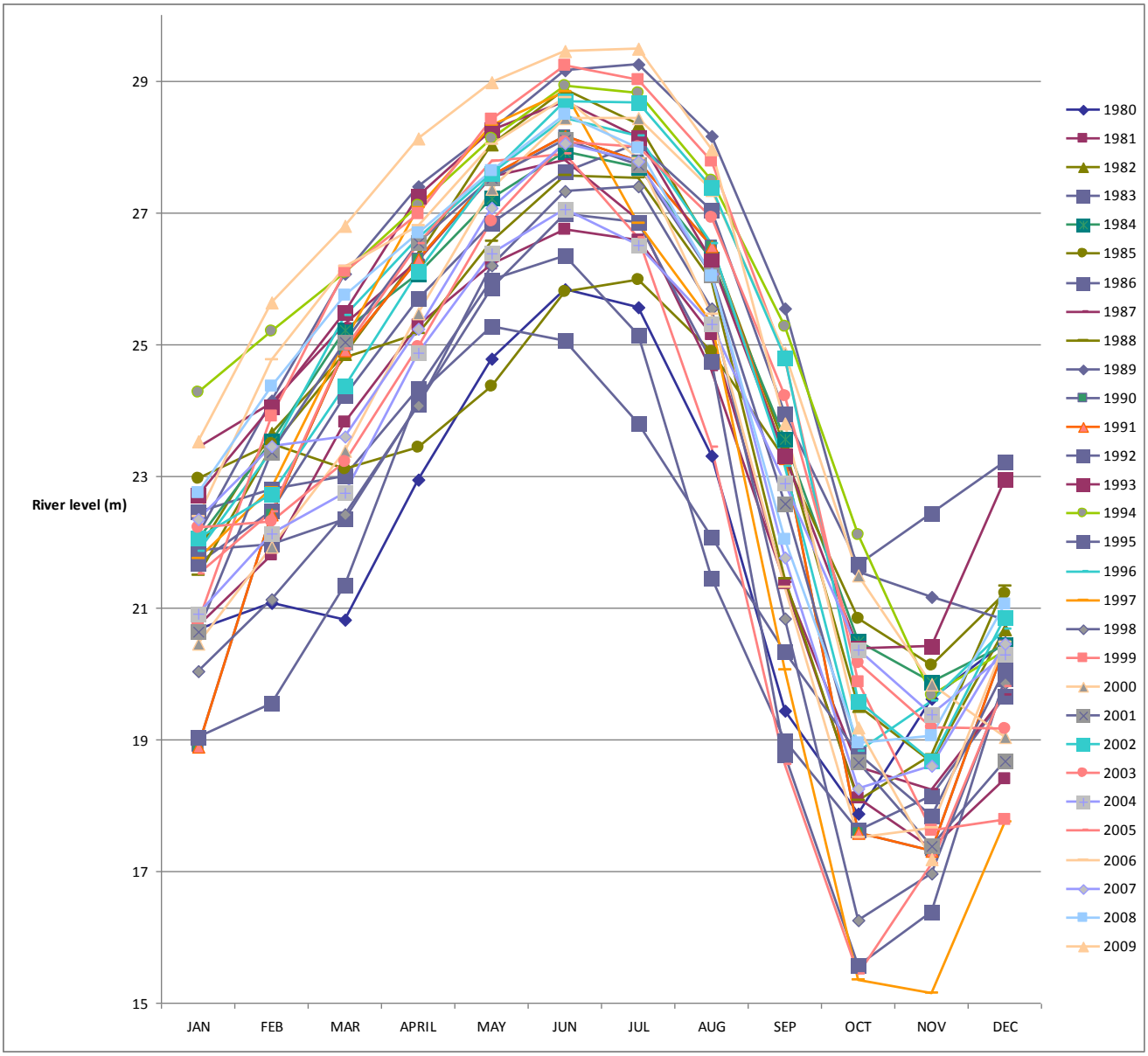
Graph based on previously unpublished data, provided by Valderino Pereira, Engenheiro, Agencia Nacional de Aguas of the Serviço Geologico do Brasil.

Fig. VII-1: Long-term Record of Rio Negro Annual High and Low Water Levels (1902-2009)



Graph based on previously unpublished data, provided by Valderino Pereira, Engenheiro, Agencia Nacional de Aguas of the Serviço Geologico do Brasil.

Fig. VII-2: Annual Variation in Rio Negro Mean Water Levels (1980-2009)



Graph based on previously unpublished data, provided by Valderino Pereira, Engenheiro, Agencia Nacional de Aguas of the Serviço Geologico do Brasil.: Graph - LemurInk

Fig. VII-3: Medium-term Records of Rio Negro Monthly Mean Water Levels (1980-2009)

3) A number of other animals (notably parrots and squirrels) also feed on seeds of immature fruits of igapó trees and, whilst competition between them and uacaris did not seem intense over the period of the current study, this may not always be the case, especially if in other years key dietary resources for

these potential competitors failed to produce abundant fruit crops. This could cause parrots, squirrels and other to feed more heavily on the fruits of the same trees species as uacaris, so driving down relative or absolute abundance of fruit crops.

In combination, these factors mean that neither the exact phenological sequence of fruiting tree species, nor the volume of their crop production is predictable on a year-to-year basis. Given that neither the availability of individual species nor their crop volume is, therefore, entirely predictable in igapó, exploiting whatever species are most abundant is a strategy likely to maximize intake, minimize travelling time and probably result in a diet varied enough to avoid accumulation of toxins that might occur if a single species were to be the focus of prolonged and focused feeding.

However, uacaris feed on a mean of 10.3 species (range 6 -17) per day, though most are at low frequency (2-10 items). This may be because, if uacaris can only exploit fruits during quite narrow periods of their maturity (Chapter 6), then the primates must test the fruits on various trees to assess if the current level of ripeness is one during which the fruits can be eaten. This is made more likely because the timing of maturation processes are also not exact, being speeded up or slowed down in response to physiological stress (e.g. Giovannoni, 2001; Lee & Bazzaz, 1982), and weather conditions.

Hence, uacaris are living in a system where resource availability varies considerably, and, in consequence, they require a flexible foraging system to accommodate this. Though relative values of available prey remain to be considered, such a foraging response is congruent with predictions of models balancing absolute and relative abundance (e.g. Charnov, 1976; Estabrook & Dunham, 1979), where a prey type is added

to the diet if its absolute abundance is greater than another prey type, as foragers choose diet items that maximize the limiting currency (considered here to be energy). The influences of handling time and nutritional value may explain variations in Ivlev Values.

7.3 *Cacajao m. ouakary* in Context: *a note of caution - inter-annual variations in phenology, spatial variation and effects of reported patterns of diet constitution*

It is only with long-term studies that the true complexity of the dietary ecology of a primate species can begin to be appreciated (e.g. Robbins *et al*., 2006: great apes; Alberts *et al*., 2005; Altmann, 1998: baboons). However, previous studies of *Cacajao* ecology prior to the current study (*C. c. calvus*: Ayres, 1986a; *C. m. melanocephalus*: Boubli, 1997a; *C. c. ucayalii:* Aquino, 1995, 1998; Aquino & Encarnacíon, 1999; Bowler, 2007) all involved less than two years of continuous fieldwork. Defler's work on Colombian populations of *C. m. ouakary* lasted for several years but nearly all data were lost when the research station was burnt by anti-government forces (Barnett *et al*., in press).

Such relatively short-term studies do not allow investigation of inter-year variation in ecology and diet, yet these are key for social and dietary ecology are intimately linked (e.g. Barton *et al*., 1996; Kunz & Linsenmair, 2008b; Swedell *et al*., 2008). Realizing that this limitation exists this is important as data from relatively short-term studies may be assumed to be typical of the species overall (e.g. Grzimek & Olendorf, 2003; Nowak *et al*., 1999; Redmond, 2008; Rowe, 1996). As recent phenological studies suggest that tropical resource availability is not as constant as was once thought (e.g. Borchert *et al.*, 2002; Noormets, 2009; Rojas-Robles & Stiles, 2009; Stevenson *et al*., 1998b), and that primate diets can vary between years (e.g. Robbins *et al.*, 2006), such assumptions may be both profound and have important consequences for conservation planning. For example, the current study shows that many of the trees at Jaú appear to have bi-annual

flowering and fruiting peaks (Section 3.6.3) which, because of methodological differences, was not revealed by previous multi-year igapó phenological studies (e.g. Maia & Pedade, 2000, 2002a,b).

Primate species show extensive variation in their diet, in some instances reflecting regional resource availability, in others apparent cultural traditions (e.g. gorillas and chimpanzees, Robbins *et al*., 2006). Though spatial variation in resource use has been demonstrated for *C. m. ouakary* (Barnett *et al.,* in press), it is hard to separate from temporal variation's confounding effects. Even when known habitat heterogeneity exists, studies have not investigated the effects of different resource patterns on diet and social ecology (for example with *C. m. melanocephalus* where populations are known to inhabit caatinga and igapó, but only the former have been extensively studied [Boubli, 1997a]). In this context, the tendency to regard one site or one study as representative of the entire species does, to quote Altman (1998: 233) ''[D]escriptions of 'typical' traits … lead too easily to typological thinking that is antithetical to the view of evolution as fundamentally a population process''.

Coherent analysis of variation in patterns of social organization and dietary ecology for all members of the genus is also confounded by the small number studies conducted and the limited number of sites at which these investigations have been undertaken. When multi-site comparisons are available for a species or species group, the extent of variation in diet becomes much clearer. Pinto (2008; Table 4.5), for example, summarizes the results of 14 longer-term diet studies on the genus *Chiropotes*, and records such extensive variation in the relative proportions of fruit, flowers and insects that only the broadest generalizations can be made without reference to the specific context in which

the observations were made. Hence, for effective conservation, there is a strong need not only for detailed long-term studies of all taxa of uacaris, but also for these to be conducted at a network of sites that cover the breadth and depth of habitat variation occupied by the genus *Cacajao.*

7.4 The Future Cacajao: consequences of *Cacajao m. ouakary* diet, conservation biogeography and evolution

Threats to the survival of primate species have been traditionally grouped into habitat loss (agriculture, extreme logging), habitat disturbance or impoverishment (selective logging, and collection of secondary forest products), and hunting (Cowlishaw & Dunbar, 2000). More recently the effects of climate change have been added (Weiderholt & Post, 2009). Below I consider the likely effects on wild *C. m. ouakary* of these impacts based on our current knowledge. Recommendations for research to help plug the gaps in our knowledge are given in Section 7.6.

7.4.1 Habitat Loss and Fragmentation

Habitat loss

Uacaris would probably fare badly in areas of extreme habitat modification. Adaptable though uacaris are in modifying their diet, this does not seem to be the kind of behavioural variability that leads to omnivory, flexible foraging and thus a capacity to survive alongside *Homo sapiens* by scavenging in the most highly human-modified environments (e.g. Ottoni & Izar, 2008: capuchins; Sapolsky, 2005: baboons). Additionally, the uacari diet is neither the foliage-dominated kind that allows howlers to survive near *H. sapiens* in plantations and urban parks (e.g. Buss, 1996; Estrada *et al.*, 1993; Printes, 1999; Williams-Guillén, 2003), nor the insect-dominated diet that (accompanied by a much smaller body size) gives some callitrichids their success in

urban environments (e.g. Gordo *et al*., 2008; Poveda & Sanchez-Palomino, 2004; Vidal & Cintra, 2006). The only pitheciines found in urban situations are *Pithecia* (da Silva *et al.,* 2007), which are of smaller body and group size than *Chipopotes* or *Cacajao*, and with a diet that has a higher percentage of leaves and insects (Norconk, 2007).

Extensive habitat loss accompanying deforestation for soya, timber or large-scale human habitation current in Amazonia (Barretto *et al*., 2008), would probably lead to extirpation of uacaris. Anecdotal reports of past distribution of *C. m. ouakary* in the Solimões-Negro interfluve, the history of settlement and growth of towns in north-western Amazonia (Cabalzar-Filho & Ricardo 1998; Little, 2001; MacCreagh, 1985; Whitehead, 2003), and the distribution of historical collection records for *C. m. ouakary* (Hershkovitz, 1987a), compared with current distributions, all suggest this to be the case. Even minimal levels of disturbance appear to cause uacaris to leave (Simone Iwanaga, pers. com.). In addition, a species which is physiologically adapted to the exploitation of unripe seeds may well lack the specialised gut flora for long-term exploitation of alternative foods such as pulp, mature seeds and leaves (Milton, 1999). Such resources are more abundant in secondary forests (Barlow *et al*., 2007; Toriola, 1998) than the immature seeds of big, slow-maturing fruits which Defler (2004), Barnett *et al.* (in press) and the current study have recorded as dominating the *C. m. ouakary* diet.

Habitat fragmentation

There have been no studies of how uacaris respond to habitat fragmentation. Gibbons & Harcourt (2009) identified primate species with greater body weights, larger group sizes, lower population densities, larger annual home ranges, slower rates of reproduction, and specialized diets and habitats as more extinction-prone and hence more vulnerable to the effects of fragmentation. Although Gibbons & Harcourt (2009) did not include *Cacajao*

among their analyses of 68 primate species. *C. m. ouakary* and other uacaris possess most of these traits, and may therefore be considered very likely to be vulnerable to the effects of fragmentation. However, some aspects of fragmentation may not affect uacaris; because of inundation tolerance and flood-related scouring, an edge community is a well-established and permanent feature of any igapó forest, with a well-defined community of species that occur only at the forest-river junction (Parolin *et al*., 2003a,b). Since this edge community is an integrated part of mature igapó, and is one which uacaris are known to exploit, the kind of edge effects so greatly increase the impact of fragmentation on terra firme forests primates (e.g. Gibbons & Harcourt, 2009) may be less likely to impact uacaris in igapó. This is all the more probable since several edge-specific species (including *Maprounea guianensis*: Euphorbiaceae; *Panopsis rubescens*: Proteaceae; *Securidaca* sp.: Polygalaceae and *Ternstroemia candolleana*: Theaceae) are present in the *C. m. ouakary* diet (Chapter 5).

There are natural mid-river islands of igapó forest, isolated year-round from other areas of igapó, and these do support populations of *C. m. ouakary* (Bezerra, 2010; Bezerra *et al*., in press). Such capacities do open the possibility that *Cacajao* might survive in fragments of 100ha or so, an identified minimum for extinction-prone species (Gibbons & Harcourt, 2009). However, the survival of such populations for multiple generations is by no means certain, for it is unknown how (or if) such populations would mitigate the stochastic effects and facilitate gene exchange. However, uacaris will forage terrestrially (Chapter 5), and in overcrowded habitat fragments species previously considered obligately arboreal have been recorded moving terrestrially from patch to patch, and foraging for extended periods on the ground (e.g. Behie & Pavelka, 2005;

Estrada, 2006; Horowich & Lyon, 1990 for *Alouatta pigra*). Thus uacaris might be able to survive mild habitat fragmentation.

7.4.2. Habitat Disturbance or Impoverishment

Commercial timber extraction

Logging of rainforests not only removes food trees (e.g. Grieser Johns, 1997: *Chiropotes*), but also alters canopy structure, changing travel times and energy budgets within a forest patch. There are also immediate and short-term direct effects (Cowlishaw & Dunbar, 2000): some species of primate have been found to be capable of adapting to the collective effects of intensive deforestation (e.g. Cabral *et al*., 2007; Ottoni & Izar, 2008; da Silva *et al*., 2007), the opportunities for a primary forest canopy-specialist, adapted to the use of large, immature seeds, appear slim.

Gathering exact data of the volumes of timber commercially exploited is difficult as much of the Amazonian timber trade and processing is done outside the legal licensing system: Laurence (1998), for example, estimated that some 80% of timber felling in Brazil was done illegally, as is some 40-50% of logging in Amazonia (Barretto *et al*., 2006). Around 50% of sawmills working in and around the state capital of Manaus operate illegally (Projeto Floresta Viva, 2006). However, of the 42 important Amazonian timber tree species listed by Witkowski (2007), eight are uacari food trees (Table VII-1). Four igapó food-tree species were among the 473 tree species listed by Erfurth & Rusche (1984) as being used for timber in Amazonia (Table VII-1). Three of these are among the most important species in the diet of *C. m. ouakary.* Terra firme diet species such as *Eschweilera corrugata*, *Inga alba*, *Manilkara bidentata* and *M. huberi* were also listed. In addition, species from a further 16 genera eaten by *C. m. ouakary* were listed, and a further 15 genera listed that were not recorded as food items but which were recorded as

occurring in the study plots (and thus possible harbingers of habitat destruction within the range of *C. m. ouakary*). A more recent study of timber use in 2003 (Lentini *et al*., 2003) lists no igapó species among the 22 principal Amazonian tree species exploited for their wood, and, though four genera in the terra firme diet were listed (*Aspidosperma, Cordia*, *Couratari* and *Manilkara*), all are minor diet items (Appendix V-1, Ch. 5), but the largely unlicensed nature of Amazonia's timber industry means it is not possible to estimate the extent to which such items are exploited. Data gathered at sawmills in Novo Airão (Rachel Lange, pers. comm.) indicated that when igapó trees were used (e.g. *Buchenavia*: Combretaceae for house foundations) it is generally only because the preferred terra firme alternative is not available.

***Table VII-1: Tree Species Used for Timber and also Eaten by* C. m. ouakary**

Latin name	***Common name***	***Habitat***	***Uacari Diet Feeding Rank (of 136)***	***Author(s)***
Micropholis venulosa	Bicó de Japó	Igapó	1	Erfurth & Rusche (1984)
Swartzia acuminatum [listed as *S. polyphylla*]	Araba	Igapó	5	Erfurth & Rusche (1984)
Various Myrtaceae	Araça	Igapó and Terra Firme	12-66	Witkowski (2007)
Macrolobium acaciifolium	Arapari	Igapó	17	Erfurth & Rusche (1984), Witkowski (2007)
Eleoloma glabrescens	Caramuri	Igapó	20	Witkowski (2007)
Manilkarna bidentata and spp.	Macaranduba	Igapó and Terra Firme	24	Witkowski (2007)
Pouteria cuspidata	Abiurana	Igapó	28	Witkowski (2007)
Calophylum brasiliense	Jacareubá	Igapó	92	Erfurth & Rusche (1984), Witkowski (2007)

Lentini *et al*. (2003) estimate that, despite comprising over some 43% of the Brazilian Amazon, exploitation is far more extensive in Pará and Maranhão states and the state of Amazonas itself contributed less than 7% of the total timber harvested in the Brazilian Amazon. Of this, Laurence (1998) considers the majority to be cut selectively. However,

there is often considerable collateral damage even with such carefully planned systems: Uhl & Kaufman (1990) studied a sustainable extraction site where 1.7% of trees were extracted, but 26% of the remainder were killed or damaged in the process. There are further collateral effects: logging teams are almost always poorly provisioned and hunt local game for protein (Barnett, 1991; Laurence *et al*., 1999b), and species that do not reach the saw mills (and so are unregistered by mill-based surveys) may be used specifically in the construction of rafts to float timber to the processing sites. Marsh *et al.* (1987) record that species used for such purposes were part of the diet of *Chiropotes.*

However, along the Rio Negro, absence of infrastructure and presence of transportation problems mean that little logging occurs outside the immediate hinterlands of towns (Barretto *et al*., 2006); and there are only six such (Manaus, Manucapuru, Novo Airão, Barcelos, Santa Isabel, and São Gabriel do Cachoeira) along the entire 920km stretch from where the Rio Negro first turns east into the Amazon basin to where it joins the Solimões to form the Amazon (Barretto *et al*., 2006). Also, a large percentage of *C. m. ouakary's* range is under some form of protection (Section 7.4.5), and logging therefore may not be carried out. However, while very few igapó trees appear as timber (Table VII-1), many are used in pallets and in plywood and chip board, the components of which are harder to trace (Eliana Andrade, pers. com.). The use of small trees (20-30cm in diameter) as wooden scaffolding in construction is common in Manaus and other cities along the Rio Negro (Fig. VII-4). Procurement of timber for this trade is indiscriminate and involves clearcutting of areas. This clearly can obviously impact negatively on uacari survival at the local level. Igapó is the commonest source of such poles (Eliana Andrade, pers. com.) Although such trees are not likely to be individuals or

species on which uacaris feed, but the trade clearly impacts the future demographic of the igapó forests affected, with a consequent diminution of habitat quality and extent for uacaris.

Fig. VII-4: Smaller Igapó Trees are Regularly Used as Construction Scaffolding in Manaus

Small-scale timber extraction

Igapó trees provide wood for local people to build and repair houses, canoes and domestic and farm implements. They also provide firewood and charcoal. Species used in this way include *Callophyllum brasiliense*, *Duroia* sp. and *Macrolobium acaciifolium* for canoes. *Inga* spp., *Sloanea guianense*, and various species of Annonaceae and Mystaceae are used for firewood and charcoal.

Secondary forest products

In Peru, Bowler (2007) noted the potential for substantial competition between *C. c. ucayalii* and humans, especially over the use the fruits of the palm *Mauritia flexuosa*, which dominates the diet of the Peruvian red uacaris and which is also an economic mainstay for many river-dwelling families. In addition, species such as *Couma macrocarpa* (Apocynaceae) which may be exploited sustainably may also be destructively harvested, to the detriment of primates for whom it served as a food source (Marsh *et al*., 1987; Peres, 1991b). However, though some fruits that *C. m. ouakary* has been recorded eating at Jaú are also eaten by local inhabitants (notably *Manilkara bidentata* and *Pouteria gomphifolia*, both Sapotaceae, and *Salacea* spp.: Hippocrataceae), such uses do not seem to be commercialized either within the park or outside it (in that such fruits rarely appear in markets and fruit stalls in regional towns). Studies at Jaú by Rodrigues (2006) identified some 120 plant species, being used medicinally, of which only six were of genera eaten by uacaris and even then these were not high ranking taxa in the *C. m. ouakary* diet (e.g. *Aspidospermum, Proteum, Salacia*, *Tabebuia*, *Tabernaemontana* and *Quinea* species). Thus it seems, based on this admittedly non-rigorous sample, that there is, at best, a limited human-uacari conflict over such species.

7.4.3 Hunting

Primates are widely hunted in Amazonian Brazil for food (Peres, 1990a, 2000a). However, unlike central and western Africa, in Amazonia there is not a substantial trade in primate flesh as 'bush-meat', where primates are shot in forests and their raw or smoked flesh then taken to towns for sale (Anadu *et al*., 1988; Brashares *et al*., 2004; Wilkie & Carpenter, 1999), though such a trade exists for other vertebrates (notably live chelonia [e.g. Conway, 2004], but also the meat of deer, tapir and caviomorph rodents:

Bodmer, 1995; Bodmer & Robinson, 2004; Wilkie & Godoy, 2001). In addition, wild-sourced fish is of great nutritional and cultural importance in Amazonia (Brown & Williams, 2003; Fa *et al*., 2002). Some 70% of the population of the Brazilian Amazon lives in towns (Barretto *et al*., 2006: data for 2001), and here consumption of monkey meat is almost always regarded as 'primitive', and to be avoided (Eliana Andrade, pers. comm.; Ariramba Sorro de Oliveira [a Ticuna Amerindian], pers. comm.; A. Barnett, unpublished data). This profound contrast with the situation in Africa is most likely to occur because large areas of Brazilian Amazon basin now lack original indigenous inhabitants living in tribal groups and conducting lifestyles in accordance with traditional views and ethics (Chibnik, 1991; Sorensen, 1967). Additionally, there is little of the interchange of individuals and culture between town and countryside that characterizes many parts of sub-Saharan Africa (Geschiere & Gugler, 1998; Gugler, 2002; Lux, 1971). At the cultural level this is mainly a result of the largely negative perception of the values of both the region's indigenous Amerindian societies and non-tribal rural inhabitants ('caboclos' or 'riberenhos': Adams *et al*., 2003; Ross, 1978; Stephen, 1993: Eliana Andrade, pers. comm.; Ariramba Sorro de Oliveira, pers. comm.). Such peoples do hunt primates, but generally for immediate consumption by the hunter's family or community or for a logging or mining camp to which they have been contracted (e.g. Barretto *et al*., 2006; Laurence, 1998; Menton, 2003). Nevertheless, such highly localized hunting can have swift and devastating effects on an area`s primate populations (Peres, 1991b).

It is the larger, more obvious, slow-breeding primate species that tend to be most vulnerable to hunting (Cowlishaw & Dunbar, 2000). Like other larger Amazonian primates, *Cacajao*'s long inter-birth intervals (2-3 years: Hershkovitz, 1987a; Barnett,

2005), late onset of sexual maturity (4 years) and single births, provide a low rate of population growth which makes them vulnerable to the impacts of hunting. However, when broad comparative multi-site studies have been undertaken in Amazonia, *Cacajao* species, in contrast to *Ateles, Lagothrix* and *Alouatta*, is never listed as a favoured hunted primate species (Parry *et al*., 2009; Peres, 1990a, 1991b, 2000a; Thoisy *et al*., 2009; Witkowski, 2007). Nevertheless, *C. m. ouakary* is hunted in some areas: with golden-backed uacaris being killed not for food but so that their meat could be used to trap other animals (Mittermeier & Coimbra-Filho, 1977), and a survey of the forests and rivers bordering Jaú found larger primates, including *Cacajao*, to be present at very low levels compared to those inside the park, and hunting was considered to be the prime factor (Simone Iwanaga, pers. comm.). At Amanã Extractive Reserve, a seven-year study estimated 120 uacaris were taken each year across the five studied communities, with *C. m. ouakary* being the third most hunted primate species after *Alouatta seniculus* and *Cebus apella* (Barnett *et al*., in press). This hunting level was, however, considered to be sustainable (Barnett *et al.,* in press). At Jaú, *Ateles* and *Lagothrix* have long been extirpated (Barnett *et al*., 2002). Hunters there (who are careful to stress that this no longer occurs) said that, when they used to hunt monkeys, they preferred *Alouatta* and *Cebus* because *Cacajao* moved too fast to ensure a secure shot (and shotgun cartridges are too expensive to waste) and, if hit, uacaris were often hard to retrieve from the water before they sank. Similar information was obtained from the Curicuriari and Uaupes rivers (Barnett & da Cunha, 1991; da Cunha & Barnett, 1990). Little information exists on hunting from the rest of the species' range, and no reports for Colombia or Venezuela.

Primates are also hunted for perceived medicinal properties (e.g. Gonzalez-Kirchner & de la Maza, 1998), although there are no reports of uacaris being are used medicinally in Jaú, or elsewhere. Rodrigues (2006) lists 29 animals used medicinally at Jaú, including two primates (*Alouatta* and *Cebus*) but not *Cacajao,* and Witkowski (2007) does not list *Cacajao* on his list of medicinal animals. The other reported use of *Cacajao* is of their bushy tails as a kind of domestic 'feather' duster (Fig. VII-5). However, animals are not killed specifically to provide these and the tails do not seem to be traded.

In summary, though hunting appears not to provide cause for concern, it is clear that there is a substantial lack of information. More information on hunting patterns is needed before hunting can be struck from the list of threats to the survival of *C. m. ouakary*

Cacacajo ouakary *tail, lower Rio Negro, 2005*

Fig. VII-5: Uacari Tails are used as Domestic 'Feather' Dusters

7.4.4 Climate Change

With few exceptions (e.g. Parolin *et al*., 2010), research predicting the effects of climate change on the vegetation of the Amazon basin have yet to include the effects on igapó, concentrating instead on entirely terrestrial habitats such as terra firme and campina, and their predicted future proportions (Chagnon & Bras, 2005; Henderson-Sellers *et al*., 1992; Huntingford *et al*., 2008; Laurence & Williamson, 2001; Laurence *et al*., 2001; Malhi *et al*., 2008; Miles, 2002). These scenarios predict increased aridity and widespread loss of both individual species and forest cover, even in central Amazonia (e.g. Malhi *et al*., 2008; Vera *et al*., 2006). For terra firme trees, Miles (2002) has predicted that, in the Rio Negro basin, 90% of species will no longer have viable populations by 2095. However, given its nature as a forest of the margins of black-water rivers, it is perhaps possible that igapó might survive better than the general Amazonian ecosystem of which it is a part.

Phylogenetic research on Amazonian plants has shown that many igapó tree species diverged several million years ago. For example, the igapó forest endemic *Swartzia laevicarpa* diverged about 3.6 Mybp from the terra firme forest species *S. benthamiana*: Torke & Schaal (2008), while igapó-living *Guatteria inundata* and *G. riparia* both split from terra firme stock between 2 and 5 Mybp, and *G. heteropetala* did so some 9-15 Mybp (Erkens *et al*., 2007a,b) Hence, if the historical ecology of such species was the same as it is now, then they have already survived several cycles of climate change, including the 6 to 8 basin-wide climatic oscillations that occurred between 15,000 and 9,000 ybp (Colinveaux, 2007), as well as the more local events 6300-5800 and 4900-3700 ybp in the western Amazon (Weng *et al*., 2002) which were part of at least six major climatic oscillations that occurred in the Holocene (Mayewski *et al*., 2004).

Several of these climatic events were extreme, highly arid and prolonged, and may have produced a savanna-and-gallery forest mosaic over large areas of the Amazon (Colinvaux, 2007; Mayle & Power, 2008), much as is being predicted for the future. This offers the possibility that igapó, in some form, might survive the forecaste climatic changes. Moreover, because hydrochoery is common, many species of igapó tree are very widely distributed (Barnett & Lehman, 2000; plus distribution maps in the various volumes of *Flora Neotropica*), facilitating down-stream recolonization. From this, it might be expected that areas of igapó would quickly establish in any areas where local water regimens permitted it, indeed the detailed palynological studies of Weng *et al.* (2002) indicate that recognizable igapó communities can form in less than 200 years.

What does this mean for the future of *C. m. ouakary* and other members of the genus *Cacajao*? Clearly, as a species that is tied to flooded forest, *C. m. ouakary* appears, at first sight, to be quite vulnerable. However, the limited association with terra firme that has been recorded at Jaú may be an artifact of the concentration of the number trees of bearing edible fruit at the study. In Colombia, *C. m. ouakary* may range for many km into terra firme when the igapó is not flooded (Defler, 1999). Similarly, Peruvian red uacaris are not flooded-forest specialists *sensu stricto* (Bowler 2007; Heymann & Aquino, in press), and *C. melanocephalus* has both flooded-forest (Lehman & Robertson, 1994a,b), and never-flooded forest populations (Boubli, 1997a). Hence, if there are sufficient resources available, future populations of *C. m. ouakary* might be found more in terra firme, especially in such areas as the Solimões-Negro interfluve where large primates specialized on eating fruit, either unripe (*Chiropotes*: Hershkovitz, 1985), or ripe (*Ateles*, *Lagothrix*: Barnett *et al*., 2002), are absent. However, given the severity of some of the

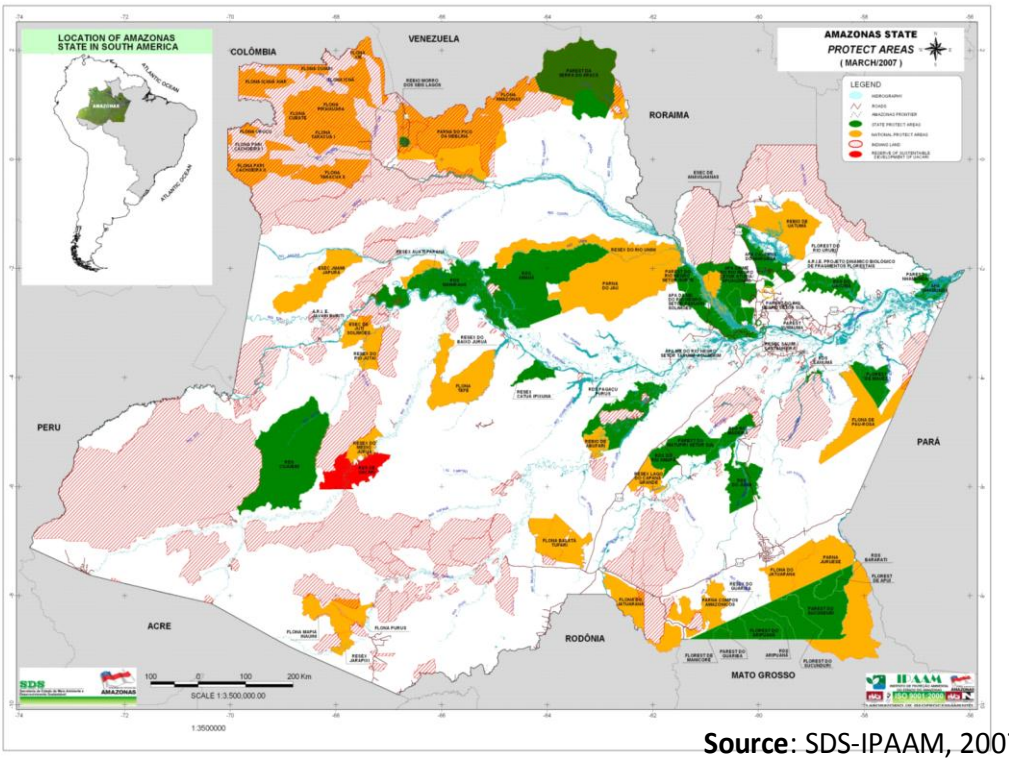
predicted outcomes of climate change, igapó may be one of the few Amazonian forest habitats to survive in any way intact, becoming the kind of gallery forest currently seen in the cerrado landscape to the south of the Amazon basin (e.g. Felfili, 1995). In such a spatially more restricted environment, with opportunities for migration to terra firme curtailed or non-existent, it might be expected that *C. m. ouakary* would move almost perpetually in smaller bands, perhaps rarely exceeding the 5-6 strong core social unit. Weiderholt & Post (2009) modeled the possible impacts of climate change on four large primate species, three of which were large and frugivorous (including the Amazonian species, *Lagothrix lagotricha*). The model predicted severe population declines for all three frugivorous species. However, Weiderholt & Post's study merely modeled increased severity of El Niño oscillations on fruit abundance and did not factor in death of adult trees as Miles (2002) had done. Combining the two studies opens the possibility that, if intact fragments of igapó survive in sufficiently large sizes to sustain them, then igapó-inhabiting primates, such as *C. m. ouakary,* and associated populations of *Cebus albifrons,* may become some of the few large primates in the Rio Negro basin not to suffer catastrophic population decline as a result of climate change.

However, such a positive scenario entirely ignores the likely human impacts, where forest products such as wood and fruits might become greatly in demand. In such circumstances, the future demands on 'igapó as Amazonian gallery forest' might best be modeled by those circumstances that currently affect the Tana red colobus (*Piliocolobus rufomitratus*), or those where competition for natural resources is even more intense, such as currently occurs in areas of the Sahel and India (e.g. Mortimore & Adams, 1999; Shiva *et al*., 1991, respectively). Destruction of its restricted habitat has put *P. rufomitratus*

among the World's 25 most endangered primates (Mittermeier *et al*., 2009), which is not an optimistic scenario for *C. m. ouakary* survival.

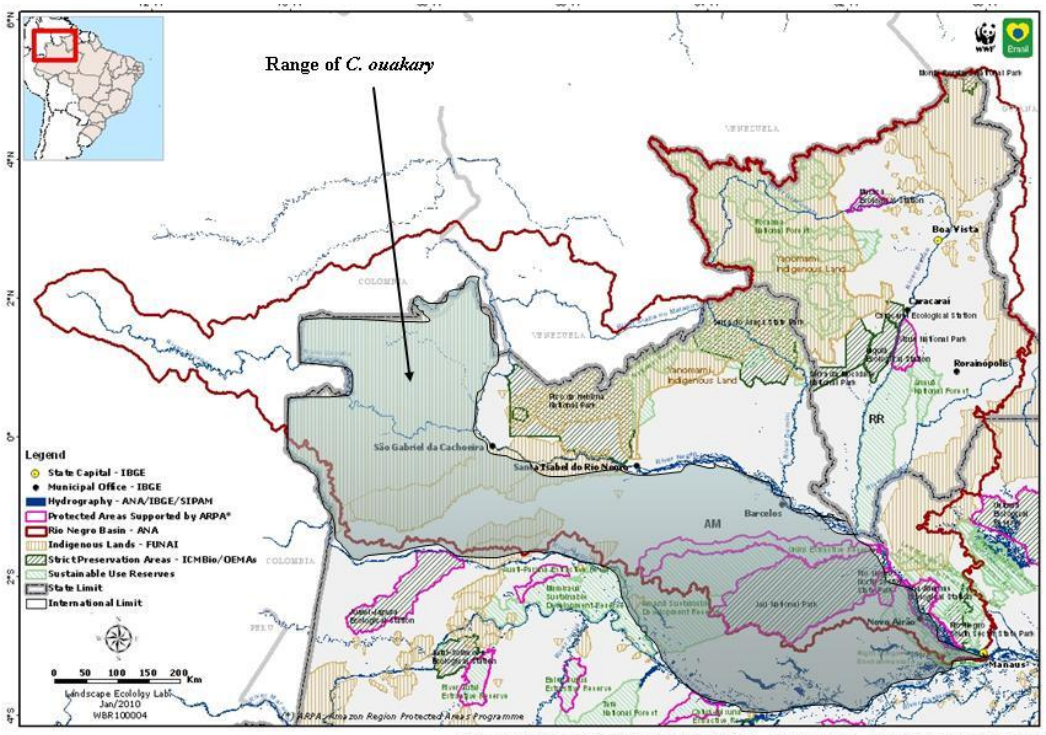
7.5.5 Conservation – Current Status and Future Trends

The current IUCN classification for *C. m. ouakary* (listed as *C. melanocephalus*, using Boubli *et al*., 2008's taxonomic arrangement) is Least Concern. In Brazil, protected areas in the upper Rio Negro basin are now well consolidated (Fig. VII-6), as a result of the Brazilian Government and WWF-Brasil's recent ARPA initiative (Silva, 2006). Here, the species' distribution currently overlaps with 10 protected areas (Fig. VII-7), totaling approx. 6,824,800ha, some 17% of the species' estimated 40,000,000ha range in Brazil, and 12.2% of the species' estimated total 56,000,000ha range (Table VII-2). Data from Colombia are less exact, but there are at least three protected areas within the range of *C. m. ouakary* there. These total 2,000,200ha (12.5% of the species' Colombian range, 3.6% of its total range). Jaú constitutes the largest single unit of protection (Table VII-2) and, as a national park, is probably the most secure, with complete bans on commercial hunting and timber extraction. Also in Brazil, Extractive Reserves (Amanã and Unini), where controlled hunting is permitted, constitute some 3 million ha of the *C. m. ouakary* range



Source: SDS-IPAAM, 2007

Fig. VII-6: Protected and Indigenous Areas in Rio Negro Basin, Brazil



Sources: Map, WWF-Brazil; *Cacajao* distribution, after Hershkovitz (1987a)

***Fig. VII-7: Overlap in Brazil between Protected and Indigenous areas in the Rio Negro basin, and estimated range of* Cacajao ouakary**

Table VII-2: Protected Areas Within the Range of C. m. ouakary

Conservation Unit	*Country*	*Area (ha)*	*% of* **C. m. ouakary** *range*	
			Country	*Total*
Parque National do Jaú	Brazil	2,368,985	5.9	4.3
Amanã Extractive Reserve	Brazil	2,233,461	5.6	3.9
Rio Unini Extractive Reserve	Brazil	833,742	2.1	1.9
Parque Estadual do Rio Negro, Setor Paduari-Solimões	Brazil	464,253	1.2	0.8
Reserva Florestal do Rio Negro	Brazil	379,000	0.9	0.7
Parque Nacional do Anavilanas	Brazil	340,831	0.8	0.6
Parque Estadual do Rio Negro Setor Norte	Brazil	148,592	0.35	0.25
Area de Proteção Ambiental do Rio Negro, Setor Tarumá-Açu Merim	Brazil	55,936	0.15	0.1
Reserva Nacional Natural Puinawai	Colombia	1,092,500	6.8	1.9
Reserva Nacional Natural Nunak	Colombia	855,000	5.3	1.6
Estacion Biologica Masiro Itajura	Colombia	52,700	0.35	0.1
TOTALS	--	8,924,000	--	16.5

Notes:
1: In addition, in Brazil, there are 10 National Forests (Cubate, Cuiari, Icná, Içana-Aiar, Paricachoeira I & II, Piraianara, Taracua I & II Uruçu and Xie). All lie within indigeous lands of the Uapes-upper Rio Negro area and so are not enumerated separatly.
2: The 620,000ha La Macarena National Park is probably extra-limital to *C. m. ouakary* westernmost range.

Within Brazil, the Rio Negro basin constitutes a bastion of tribal power and culture (Kennedy & Perz, 2000; Silva *et al*., 2007), with 11 million ha under tribal control (Fiona Watson, pers. comm.). Of this, some 7 million ha land occurs within the Brazilian range of *C. m. ouakary*, including the Iaunetê and Pari-Cachoeira Indigenous Areas (figs. VII-6, 7). Concentrated in the western part of *C. m. ouakary's* Brazilian range, these areas overlap completely with the 10 national forest areas (the 'FLONAS' in Fig. VII-6, see Note 1, Table VII-2). In the areas under indigenous control, hunting and extraction of rainforest products occurs, but external commercial exploitation is unlikely (Bodmer, 2006; Cormier, 2000; Naranjo *et al*., 2004; Silvius *et al*., 2004).

Combining protected areas and indigenous areas, the area under management is some 16,000,000ha, or about 28.6% of the estimated total area potentially occupied by *C. m. ouakary*. Whilst this is extremely positive, it should be realized that, such a broad figure

takes no account of variations of habitat quality, and the current and past hunting and other land manegement practices may have interacted to produce variations in *C. m. ouakary* population densities over its extensive range. Nor is it guaranteed that the densest or most viable populations occur within existing protected areas.

It is notable that, despite its current IUCN status, the true on-the-ground situation of wild *C. m. ouakary* populations is unknown in any part of its range except some small sectors of Jaú and the Amanã Extractive Reserve, and some small areas of Colombia. The species' status and the existence (or otherwise) of threats, and how these might be trending, have not been surveyed in any of the other protected areas in its range, nor have the distributional limits, population densities, threats or their trends been assessed in relation to this species. Thus, though the area that is protected in some form is substantial, the value of such protection and the size and disposition of the *C. m. ouakary* populations within these area, and the threats facing them there, have yet to be assessed in anything beyond the most cursory form.

7.5 New Developments in *Cacajao* Taxonomy: biogeographical considerations and the possibility of sub-species within the known range of *C. m. ouakary*

Distribution maps in Hershkovitz (1987a) show the known range of *C. m. ouakary* (= *C. ouakary* of Ferrari *et al*., 2009, 2010) extending along the entire Solimões-Negro interfluvial and westwards to the foothills of the Colombian Andes. Combining this with further data on the western part of the species' range (Defler, 2004), gives a distribution of *C. m. ouakary* extending 1200km east to west and covering an approximate area of some 560,000km² (an area slightly larger than France). At first glance, this is one of less ample ranges for Amazonia's larger primate species (dwarfed, for example, by the extensive ranges of several members of the genera *Alouatta, Ateles, Cebus, Chiropotes*,

Lagothrix and *Pithecia*: Eisenberg & Redford, 1999). However, unusually for an Amazonian primate, the golden-backed uacari is currently regarded as monomorphic. Analysis of primate distribution patterns by Ayres & Clutton-Brock (1992) showed that large and/or fast-flowing rivers were prime distributional barriers between congeneric Amazonian primates, supporting the original contention of Wallace (1852) that rivers acted as isolating mechanisms for Amazonian primates and other non-volant fauna. It is therefore not too surprising that, within the ranges of these widely-spread Amaonzian primates there is often considerable genetic structuring, resulting in sub-species and otherwise distinct populational level (e.g. Gregorin, 2006, Harris *et al*., 2005 for *Alouatta* species: Cruz-Schneider *et al*., 2005 for *Aotus*: Di Fiore & Fleischer, 2005; Ruiz-Garcia, 2005 for *Lagothrix*; Defler, 2004, for reviews up to 2003).

As shown by Ferrari *et al.*'s (2009, submitted) reinterpretation of the work of Boubli *et al.* (2008), and Bowler *et al*. (2009) new *C. c. ucayalii* range discoveries, it seems plausible that smaller rivers than those identified by Ayres & Clutton-Brock may also act as sufficient barriers for genetic differentiation to occur to sub-species level in some species of larger Amazonian primate, including *Cacajao*. The range of *C. m. ouakary* includes several large rivers such as the Curicuriari and Uaupes in Brazil, and the Vaupes and Guainia in Colombia, and the presence of the the last of the Andean foothills around the Guiavire, Inirida and Vaupes could also impede genetic flow between western-most populations of *C. m. ouakary*. In addition, the influence of past climatic events must be considered: the northeastern area of the Amazon has long been recognized as one with a high proportion of endemics and, though some apparent endemics have been shown by later work to have a broader distribution that previously supposed (e.g. Borges, 2004),

there is strong evidence of disjunct faunal distributions in the region (Borges & da Silva, in press; Valenzuela, 2001). These are congruent with the distribution of extensive natural areas of non-forest vegetation in the upper Rio Negro area, especially the Uaupes river basin (Anderson, 1981), areas which are extensive now, but which may have been even greater in the past (Cracraft, 1988, 1994; Defler, 2004); possibly one that was sufficient to provide barriers to gene flow between isolated populations (Borges & da Silva, in press). The possibility that these may also be reflected in genetic structuring in the *C. m. ouakary* and that the golden-backed uacari populations in Colombia and the upper Rio Negro are sub-specifically different from those on the lower Rio Negro should be investigated using mtDNA studies of museum specimens supplemented by fæcal and hair samples from existing populations.

7.6 Recommendations for Future Research on *C. m. ouakary*

The following ecological studies should be conducted at a minimum of three sites across the range of *C. m. ouakary*, and be part of a long-term research programme:

Social ecology

- tag individual uacaris for identification so that group composition and ranging can be unambiguously studied
- radio-track individual animals with satellite-linked GPS systems to establish daily and seasonal movements
- attempt to obtain full-day follows, the better to define the daily time budget and perhaps understand why uacaris move so fast and feed for such short periods in single patches
- gain a better understanding of social behavior, the causes of the apparent lack of aggression and the nature of social structure and between-group migration pattern

Dietary ecology

- use an expanded system of 1 ha, 10cm minimum DBH phenological study plots that will include igapó, terra firme close to and 1 and 2km distant from the river margin as well as plots in minor habitats (such as *Mauritia flexuosa* swamps and caampina)
- track not only phenology on a monthly basis, but the chemical ontogeny of fruits of tree species in the various habitats. Crop volume should also be monitored monthly and studies should be arranged to allow for inter-year differences in flowering and fruiting intensities to be tracked
- test for fruits of Jaú's terra firme and igapó Schaefer *et al.* (2002)'s observation that the calorific content of fruits and seeds increases with their maturity
- monitor contemporaneously the diet of parrots, squirrels and other primates to establish the framework of competitive interactions
- study effects of commensal ants and insect larvæ within seeds on choice ratios of diet species.

Conservation-related activities

Across the range of the species, the following should be initiated:

- surveys of uacari densities inside and beyond the boundaries of all major protected areas within the species rang
- conduct these using surveys of the major rivers in Negro-Solimões interfluve to establish distribution and densities of *C. m. ouakary* populations in Brazil,
- above to be combined with surveys of genetic structuring of *C. m. ouakary* populations in Brazil, Colombia and Venezuela.

- above to be combined with surveys of genetic structuring of populations in Brazil, Colombia and Venezuela
- range-wide surveys of human hunting practices and use of secondary-forest products as well as collation of actual and projected patterns of timber-extraction in both terra firme and igapó throughout the species range
- combine above with range-wide quantitative surveys of igapó to permit assessment of variation of densities, relationship between primate densities and igapó species composition and the identification of key diet species and aspects of habitat quality to aid in conservation planning.

In combination, all of the above to allow identification of areas of high-quality igapó for future conservation projects using golden-backed uacari as a flagship species and help secure the continued survival of the remarkable primate and its extraordinary habitat.

APPENDICES

Chapter 2: Appendices

Appendix II-1: Expects Who Identified Plant Species from Digital Images.

African violet family (Gesneriaceae, Christian Feuillet, Smithsonian Institution, Washington DC), Brazil nut family (Lecythidaceae: Scott Mori, New York Botanic Garden), mistletoes (Loranthaceae and Viscaceae: Job Kuijt, U. Victoria, Canada), myrtles (Myrtaceae, *Myrcia, Marlierea, Plinia, Psidium*: Evelyne Lucas, Kew: *Eugenia,* Bruce Holst, Selby Botanic Gardens, Florida), Sapodillas (Sapotaceae: Aparecida Donisete de Faria, INPA and Toby Pennington, Royal Botanic Gardens, Kew), and various sections of the pea family (Fabaceae: Mike Hopkins, INPA), the Legume genera *Inga* (Toby Pennington, Royal Botanic Gardens, Kew), and *Sclerolobium* (Vidal de Freitas Mansano, Jardim Botânico do Rio de Janeiro), Passion flowers (Passifloraceae, Christian Feuillet, Smithsonian Institution, Washington DC), Protea family (Proteaceae: Leandro Ferreira, Museu Goeldi, Belém, William Milliken, Kew, Ghillian Prance, Kew). Ricardo Braga-Neto (INPA, Botany) identified fungal samples.

Appendix II-2: Experts Who Identified Animal Species from Digital Images

Ambylopygid: Linda Raynor (U. Cornell, USA), Ephemeroptera: Eduardo Domínguez and Carlos Molineri (Universidad Nacional de Tucumán, Argentina), Lepidoptera: Dick Vane-Wright (University of Kent Canterbury), Orthoptera: George Beccaloni and Judith Marshall (The Natural History Museum, London).

Appendix II-3: Sources Used to Assess Tree Sex-ratios for Crop Volume Estimates

Family	*Author*
Annonaceae, *Duguetia*	Maas *et al*. (2003)
Chrysobalanaceae	Prance (1972a)
Fab.: Caes., *Swartzia*	Cowan (1967)
Fab.: Mim., *Parkia*	Hopkins (1986)
Lecythidaceae (zygomorphic)	Mori & Prance (1990)
Olacaceae	Sleumer (1984)
Sapotaceae	Pennington (1990)

In addition, these general Amazonian floras were consulted:
Brako & Zarucchi (1993), Gentry (1993) and Ribeiro *et al.* (1999).

Chapter 3: Appendices

Appendix III-1: Numbers of Trees, Palms and Lianas by Species in Survey Quadrats at Jaú National Park

Key: *IG=igapó quadrats, 3,7,8, are progressively distant from the terra firme shore. PG = quadrats at the margin of igapó, next to the river's main body. Borok = Borokotò, a swamp forest with dryland hummocks, TF = terra firme (never-flooded) forest, CAP = capoeira (secondary forest, 15 years old in this sample).*

SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Acosmium nitidens	Fab-Pap	1	1		5	6			
Aldinia heterophylla	Fab-Caes						2	3	
Alibertia edulis	Rubi				3				
Alchorea sp.	Euph								1
Alchorneopsis sp.	Euph								3
Amaioua guainenensis	Rubi						2	1	
Amanoa oblongifolia	Euph	82		41	24	3			
Anacardium parviflorum	Anac							1	
Andira unifolia	Fab-Pap						2		
Aniba sp.	Laur	1	8						
Aniba sp. 1 'plumbea'	Laur		1						
Aniba ferrea	Laur						10	2	1
Aniba williamsi	Laur							1	
Aparisthium cordatum	Euph								3
Apeiba echinata	Tilia							1	
Aspidosperma schultesii	Apoc.							3	
Astrocaryum jaori	Arec					2			
Astrocaryum aculeatum	Arec								8
Attalea maripa	Arec						11		
Batesia floribunda	Fab-Caes						1		8
Bellucia grossulariodes	Mela								1
Bertholecia excelsa	Lecy								9
Bocageopsis muliflora	Annon							2	
Bogageopsis pleiosperma	Anno						1		
Brosimum parinaroides	Mora						2	1	
Brosimum rubescens	Mora						2		
Buchenavia grandis	Comb						1	1	
Buchenavia ochrograma	Comb		91		1	1			
Buchenavia parviflora	Comb							1	
Buchenavia sp.	Comb							1	
Burdachia prismatocarpa	Malph	5	14		11	1			
Calophyllum brasiliense	Clus						1		
Caraipa grandifolia	Clus						6		
Caryocar glabrum	Cary							1	
Cedrelina sp.	Fab-Mim						1		

Appendix III-1: Numbers of Trees by Species in the Survey Quadrats – continued 1

SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Casearia marquitensis	Flac							1	
Casearia sp.	Flac		3						
Cipo d'agua *(Doliocarpus rolandri)*	Dill						5		
Cipo buxexa de velha			6						
Cipo escada de jaboti *(Bauhinia rutilans)*	Fab-Caes							1	
Cipo pe de galhinha			1						
cipo tucunare		4	10						
cipo jurua							5	1	
cipo sp.		1					1		
cipo sp. 1							1		
cipo sp. 3							1		
cipo sp. 4							3		
cipo sp. 5							1		
cipo sp. 6							1		
cipo sp. 7							1		
cipo sp. 8							2		
cipo sp. 9								1	
Chrysophyllum sanguinolentum	Sapot						1	4	
Chrysophyllum prieurii	Sapot						2		
Chrysophyllum sp.	Sapot						1		
Clathrotropis nitida	Fab-Pap				4	5			
Clusia sp.	Clus						1	6	
Conceveiba martesiani	Euph							1	
Cordia exalta	Borag		5				1		
Couma utilis	Apoc.						1		
Coupeia bracteata	Chrys						2		
Coupeia comomensis	Chrys							5	
Coupeia paraensis	Chrys	1				5			
Crudia amazonica	Fab-Pap	1							
Cybianthus fulvopulverulentus	Myrs				7	10			
Dead tree		5						3	5
Dacryodes sp.	Burs						4	2	
Dialium sp.	Fab-Caes					2			
Dialium guianensis	Fab-Caes							1	3
Diospyros cavalcantes	Eben				2	17			

Appendix III-1: Numbers of Trees by Species in the Survey Quadrats – continued 2

SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Diospyros manuaensis	Eben							1	
Dipteryx odorata	Fab-Pap								1
Dipteryx polyphylla	Fab-Pap						1		
Dipteryx punctata	Fab-Pap						1	1	
Discocarpus spruceanum	Euph	3			2	8			
Doliocarpus brevipedicellatus	Dill						1		7
Duguetia sp. 1	Annon		3		1				
Duguetia estrelachanta	Annon							1	
Dulacia sp.	Olac				1				
Duroia velutina	Rubi		1		20	5			
Erisma unicinctum	Voch							2	
Eleoloma glabrescens	Sapot	12	4	44	5	27			
Endlicheria chalisa	Laur				2	5			
Erythroxolon sp	Eryth				4				
Erythroxolon sp 1	Eryth						1		
Eschweilera sp.	Lecy						2		
Eschweilera alba	Lecy		17						
Eschweilera bracteosa	Lecy							1	
Eschweilera pedicillata	Lecy							2	
Eschweilera tenuifolia	Lecy	9		112	2	14			
Eschweilera tessmannii	Lecy						3	2	
Eschweilera truncata	Lecy						4	2	1
Eschweilera wachenheimai	Lecy							7	
Eugenia cuspidifolia	Myrt							1	
Eugenia florida	Myrt							1	
Eugenia cf. longiracemosa	Myrt				1				
Eugenia gomesiana	Myrt					2			
Eugenia omissa	Myrt							1	
Eugenia sp.	Myrt				1	1			
Eugenia sp. 1	Myrt		1		11	11	2	1	
Eugenia sp. 2	Myrt				1	2			
Eugenia sp. 3	Myrt				3				
Eugenia sp. 4	Myrt								
Eugenia sp. 5	Myrt				1	1			
Eugenia sp. 6	Myrt					1			
Eugenia sp. 7	Myrt					2			
Euterpe precatoria	Arec						2		6

Appendix III-1: Numbers of Trees by Species in the Survey Quadrats – continued 3

SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Ferdinandusa hirsuta	Rubi							2	
Ferdinandusa sp.	Rubi							2	
Gaustavia elliptica	Lecy						4	17	
Gautteria foliosa	Anon							1	3
Gautteria olivacea	Anon							1	
Gautteria sp.	Anon		1			14			
Gautteria sp. 1	Anon		1				1		
Genipa sp.	Rubi					1			
Goupia glabra	Cela								4
Hebepetalum humifolium	Lina							1	
Helicostylis scabra	Mora						2	1	2
Hevea brasiliensis	Euph						1		
Hevea spruceanum	Euph	4		10		1			
Himatanthus bracteatus	Apoc.				2				
Himatanthus sucuuba	Apoc.								1
Hirtella sp.	Chrys		9	1					
Histeria barbata	Olac						2		
Histeria spruceana	Olac					3			
Homalium guianense	Flac	2	1						
Homalium racemosum	Flac	18							
Hydrochorea marginata	Fab-Pap	13	3	40	2	1			
Inga sp.	Fab-Mim						1		3
Inga sp. 1	Fab-Mim								1
Inga obidensis	Fab-Mim							2	1
Inga bicoloriflora	Fab-Mim							2	
Iryanthera sp.	Myris						1	1	
Iryanthera juruensis	Myris							1	
Iryanthera laevis	Myris							1	
Iryanthera paradoxa	Myris						1		
Iryanthera paraensis	Myris							1	
Iryanthera ulei	Myris						1	1	
Iserta sp.	Rubi						1		
Iserta hypoleuca	Rubi						1	1	
Jacaranda copaia	Bign						1		
Lecythis pisonis	Lecy							1	
Lecythis zabuco	Lecy						1	2	
Lacistema grandiflorum	Laci								1
Lacmellea sp.	Apoc.	3			4	6			

Appendix III-1: Numbers of Trees by Species in the Survey Quadrats – continued 4									
SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Lachmellea arborescns	Apoc.							1	6
Leonia cymosa	Viol						1	2	
Leopoldinia pulcra	Arec					7			
Licania apetala	Chrys						4		1
Licania 'folhas coriaceas'	Chrys					1			
Licania hirsuta	Chrys						1		
Licania impressa	Chrys							2	
Licania laevigata	Chrys						2		
Licania heteromorpha	Chrys	14	12				5		
Licania latifolia	Chrys							1	
Licania micrantha	Chrys						1		
Licania mollis	Chrys				2	1	1		
Licania oblongifolia	Chrys						5	2	
Licania palliata	Chrys						1		
Licania sprucei	Chrys						1		
Licania sp.	Chrys	2					3	3	
Licania sp. 1	Chrys				2				
Licania sp. 2	Chrys					6			
Licaria sp.	Laur				4	1		1	
Licaria guaianensis	Laur						2	1	
Mabea nitida	Euph	61	1	12	1				
Macrolobium acaciifolium	Fab-Mim	3		12	1	1			
Macrolobium limbatum	Fab-Mim						1		
Maloueta flavescans	Apoc.		5	1		1			
Maprouna guianensis	Euph		1		2	15			8
Matayba sp.	Sapot								1
Miconia argyophylla	Mela								12
Miconia poeppigii	Mela								11
Miconia regalli	Mela							1	1
Miconia sp.	Mela							1	
Micropholis g. duckei	Sapot							1	
Micropholis g. guineanensis	Sapot							11	
Micropholis venulosa	Sapot		1		15	23	2		
Micropholis sp.	Sapot						2		
Minquartia guianensis	Olac						1		
Mollia speciosa	Tilia				1				
Mouriri guianensis	Myrt	3			1	1			

Appendix III-1: Numbers of Trees by Species in the Survey Quadrats – continued 5

SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Mouriri huberi	Myrt						1		
Mouriri torquata	Myrt							1	
Myrcia cf. grandis	Myrt		23			8			
Myrcia paivae	Myrt		12	1					5
Myrciara vismifolia	Mryt				3				
Neea madeiruna	Nyct							1	
Neea sp.	Nyct							2	
Ocotea sp.	Laur	1				1			2
Ocotea sp. 1	Laur							1	1
Ocotea sp. 2	Laur							2	
Ocotea guianensis	Laur						1	1	
Ocotea nigrescens	Laur								9
Ocotea nitida	Laur							3	
Odontdenia punctulosa	Apoc.								9
Oenocarpus bacaba	Arec						4	7	
Orbogmya speciosa	Arec								1
Ormosia paraensis	Fab-Mim	4	3	3	4				
Osteophloem platyspermum	Myris							1	
Ouratea sp.	Ochn	1			2				
Pagamea sp.	Rubi							1	
Panopsis rubescens	Prot				2				
Parahancornia fassiculata	Apoc.						1		
Paraqueiba sericea	Icac								1
Parkia discolor	Fab-Mim					1			
Parkia panuresis	Fab-Mim								3
Paypayrola grandiflora	Viol							1	
Pera bicolor	Euph						1		
Pourouma nata	Mora							4	
Pourouma cuspidata	Mora							1	
Pourouma tomentosa	Mora							1	
Pourouma minor	Mora							2	
Pourouma sp.	Mora							1	
Pouteria anomala	Sapot						1		
Pouteria auripaniculata	Sapot							3	
Pouteria caimito	Sapot						1		
Pouteria elegans	Sapot	105	18	20		3	1		
Pouteria gomphophyllum	Sapot		7						

Appendix III-1: Numbers of Trees by Species in the Survey Quadrats – continued 6									
SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Pouteria macrophylla	Sapot						2		
Pouteria sp.	Sapot	2					6		
Pouteria sp. 2	Sapot							2	
Protium amazonicum	Burs							3	
Protium apiculatum	Burs						2	5	
Protium crassipetalum	Burs						3	2	
Protium decandrum	Burs						4	1	
Protium ferrugineo	Burs							2	
Protium grandiflorum	Burs							2	
Protium paniculatum	Burs						2	3	
Protium trifoliatum	Burs						1		13
Pseudoxandra coriacea	Annon							1	
Pterocarpus sp.	Fab-Pap						1		
Qualea paraensis	Voch						1	1	
Qualea sp.	Voch						1		
Quinna negrensis	Quin					1			
Rollinia insignis	Anno						1		
Roucheria pantata	Lina							1	
Sacoglottis mattogrossensis	Humi						1		
Sacoglottis guinensis	Humi				1				
Sacoglottis sp.	Humi				3				
Schefflera sp.	Arel						3	1	
Sclerolobium hypoleuca	Fab-Caes		7		23	11			
Sclerolobium melanocarpum	Fab-Caes							1	1
Sclerolobium sp.	Fab-Caes				8				4
Sclerolobium sp. 1	Fab-Caes							2	
Simaba orinocensis	Sima				2				
Simaba polyphylla	Sima						3		
Sloanea latifolia	Eleo						1		
Sloanea sp.	Eleo							1	1
Socratea exorrhiza	Arec								7
Spathelia excelsa	Ruta							5	
Stryphnodendron guianensis	Fab-Mim						1		
Swartzia corrugata	Fab-Pap								1
Swartzia ignifolia	Fab-Pap							1	
Swartzia laevicarpa	Fab-Pap				2				

Appendix III-1: Numbers of Trees by Species in the Survey Quadrats – continued 7

SPECIES	***Family***	***IG-3***	***IG-7***	***IG-8***	***PG1***	***PG2***	***BOR -OK***	***TF***	***CAP***
Swartzia panacoco	Fab-Pap						2	4	2
Swartzia polyphylla	Fab-Pap					1	2	3	
Swartzia recurva	Fab-Pap						2	1	
Swartzia tomentifolia	Fab-Pap						9		
Swartzia sp.	Fab-Pap						5	8	
Symphonia globulifera	Clus							1	
Tapirara obtusa	Anac						2		11
Tapura amazonica	Dich							1	
Tabebuia barbata	Bign				1	3			
Tabernaemontana sp.	Apoc.		3	8					
Taralia oppositifolia	Fab-Pap						1		
Ternstroemia candolleana	Thea		1		16	9			
Toulicia guianensis	Sapin							2	1
Theobroma silvestre	Ster							3	
Tovomita schomburgkii	Clus							1	
Trattinnickia burserifolia	Burs						1		1
Trattinnickia roifolia	Burs						1		
Unidentified			2						
Vantanea sp.	Humi						1		1
Virola caducifolia	Myris							1	
Virola calophylla	Myris						1	1	
Virola mollissima	Myris							2	11
Virola pavonis	Myris						1		
Virola sp.	Myris					6		1	
Vismia cayennensis	Clus							1	
Vismia guianensis	Clus							1	
Xylopia nitida	Annon						1		
Zygia ramiflora	Fab-Mim						1		

Appendix III-2: Number of Species per Family per Habitat

(** in some instances a species occurred in both igapó and terra firme)*

Family	***All habitats****	***Igapó***	***Terra firme***
Anacardiaceae	2	0	2
Annonaceae	11	3	9
Apocynaceae	10	4	6
Arecaceae	8	2	6
Areliaceae	1	0	1
Bignoniaceae	2	1	1
Boraginaceae	1	1	1
Burseraceae	11	0	11
Caryocaraceae	1	0	1
Celastraceae	1	0	1
Chrysobalenaceae	19	8	14
Clusiaceae	7	0	7
Combretaceae	4	1	3
Dillenaceae	1	0	1
Ebenaceae	2	1	1
Eleocarpaceae	2	0	2
Erythroxylaceae	2	1	1
Euphorbiaceae	11	5	7
Fab-Caesalpinoidae	8	3	6
Fab-Mimosoidae	10	2	8
Fab-Papilionoidae	20	7	14
Flacourtiaceae	4	3	1
Humiriaceae	4	2	2
Icacinaceae	1	0	1
Lacistemaceae	1	0	1
Lauraceae	12	4	10
Lecythidaecae	12	2	10
Linaceae	2	0	2
Maphphigiaceae	1	1	0
Melastomataceae	5	0	5
Memyclaceae	3	1	2
Moracaeae	8	0	8
Myristicaceae	13	2	12
Myrtaceae	16	12	5
Nyctagenaceae	2	0	2
Ochnaceae	1	1	0
Olacaceae	4	2	2
Proteaceae	1	1	0

Appendix III-2: **No. of spp. /family / habitat – continued 1**

Family	***All-habitats***	***Igapó***	***Terra Firme***
Rubiaceae	9	3	6
Rutaceae	1	0	1
Sapindaceae	1	0	1
Sapotaceae	18	6	14
Simabouraceae	2	1	1
Sterculiaceae	1	0	1
Theaceae	1	1	0
Tiliacaea	2	1	1
Violaceae	2	1	1
Vochysiaceae	3	0	3

Chapter 4: Appendices

Random Numbers Generated at www.random.org to Create Data for Statistical Testing of Differences between Sleeping Trees and a Random Selection of Igapó Trees (for Section 4.3.5)

(The program was tasked to generate 20 random numbers between 1 and 359 and 30 random numbers between 818 and 1320. These were the plot numbers for igapó quadrats 3, 7 and 8. Thirty nine of the 50 generated numbers were used (16 of the first series and 23 of the second: these proportions being equal to their share of the sample)

1	285	21	340	158	245	87	57	311	275	126
2	63	340	94	72	101	244	117	97	144	63
3	1032	986	1202	1045	1069	916	1119	907	1181	999
4	1209	1093	885	1136	1036	884	854	846	1081	1148
5	1032	1165	1051	952	1291	1000	1237	1073	1090	1297

Appendix IV-2: Observed Behaviours of Cacajao ouakary, *not Associated with Foraging, Movement or Feeding*

Behaviour	***Context***
Reaction to calls of another group	On one occasion the Parana group heard the Ilha group giving 'chock' calls and became extremely agitated. Because of the lack of individual identification and the fluid nature of group composition, groups were defined by geographical location rather than composition. Thus, the possibility that two small group met without calling is high. No such reactions were observed when the same group heard calls of *Alouatta* or *C. albifrons* groups.
Fighting	I did not directly observe fighting. Two adult-sized individuals were once observed chasing each other with what appeared to be aggressive intent, but this could have been play. Fighting is reported by Bezerra *et al.* (submitted) as rare in this uacari.
Threat display to uacari	Turning to face perceived intruder with moderate piloerection and vigorously flicked tail. Accompanied by *Trill* and *Cough* vocalizations. Observed on four occasions when animal from one foraging sub-group tried to cross into tree occupied by mother and baby (2), and mother and baby and presumed older offspring (2) of another. The interloper retreated on each occasion.
Threat display to observer	A Brazilian biologist field assistant witnessed an adult make breaking branches in front of her. I had a female pass over the canoe and defecate on top of me. Another uacari urinated close to the canoe. On five occasions (after habituation) large adults stood their ground once the group had gone and looked directly at me with fluffed up body hair. In three cases the tail was held erect, in two it was held to the side and was curved forwards.
Threat to other species	On five occasions groups of *C. ouakary* and of *S. sciureus* (3) or *C. albifrons* (2) were observed to encounter each other while foraging-moving with a distance of less than 10m between the outermost members of each group. In each case the uacaris acted aggressively: to the capuchins some members began pumping branches with their arms and limbs, piloerectijng and making *chock* vocalizations. Reactions to the squirrel monkeys were less intense, with *chock* vocalizations and some short rushes towards them. There were no such reaction when the groups were more widely separated.
Play	Play was noted between sub-adults and between sub-adults and juveniles. Four behaviours were considered to be play: chasing, wrestling, leaping (either alone or in company), and trapeze (where one animal dangled from another's arms or legs).

Appendix IV-2: Observed Behaviours of Golden-backed Uacaris – continued 1

Behaviour	***Context***
Grooming (self)	Allogrooming was observed very rarely, being only encountered 14 times. It was never extensive but involved brief (6-10 secs) rummaging and stroking of pelage with hands. This was observed for flank (4 times), tail (4 times), legs (6 times). In each case this occurred while the animal was resting during the day. On two other occasions foraging animals licked their lower arms and hands (possibly to remove gum or ants?), and on one additional occasion an animal picked at its mouth with its fingers (possibly for the same reason).
Grooming (conspecific)	This was observed only twelve times between and always between adolescents or sub-adults. In each case the animals were resting during the day and were proximate in a tree. Grooming was dyadic in four events, with the animals facing each other, and in three others the back of one was groomed by another. In one event three animals sat behind each other in a row, two each grooming the other animal sitting immediately in front. Grooming sessions lasted 14, 17, 21, 25, 27, 34, 42 and 44 seconds. It was not possible to sex the animals, but they were, in each case, the same size and had been travelling closely together prior to settling down to rest. In four other events the exact nature of the interaction was obscured by vegetation, though arm movements showed grooming was clearly in progress. No vocalizations were detected associated with the grooming.
Touching infant of other individual	Young uacaris usually stayed close to the presumed mother (Table IV-24). However, on two (possibly three) occasions, adult-sized individuals came close to an infant and touched it with their hand while the mother was foraging. Having approached stealthily, they then quickly retreated. The significance of this is obscure.
Sexual display	On a singe occasion a (young?) male ran and leapt through a group of feeding adults with an erect penis. He strove to remain his body as vertical as possible during the display. The shaft of the penis was black, the head a bright pink. No obvious precipitating incident preceded this display, which appeared to neither accompanied nor followed by any specific vocalization.
Scent marking	On two occasions adult females were seen to adopt a semi-squatting posture and rub their anal areas along the bark of large horizontal branches. The areas were not immediately investigated by other animals in the group and no obvious behaviour immediately preceding provoked this. On two other occasions, animals resting prone of a branch made rubbing movement of the chest. In neither case was it certain that this was scent marking as it was impossible to access the branches to see if glandular exudates had been deposited.
Vine swinging	One three occasions adult individuals, lagging behind a fast moving group, were seem to swing back-and-forth on a long vertically-hanging vine before letting go at the acme of its arc. This appeared to aid in the crossing of a wide gap. The distances crossed in this way were: 8, 9 and 13m. Uacaris can make leaps of around 6m unaided.
swimming	On two occasions individuals who fell into the water while foraging were seen to swim doggy-paddle style to the nearest trunk and ascend.

Appendix IV-3: Interactions Between Uacaris and Other Primates

Primate Species	***No. of Uacaris***	***No. of Individuals of Other Primate Species***	***Type of Interaction***	***Duration***
Alouatta seniculus	22	5	In terra firme, band of uacaris in transit passed within 20m of group of feeding uacaris. Howlers initially piloerected and rumbled a little. Uacaris made no observable response.	8 mins (for full passage of group)
Alouatta seniculus	31	5	In terra firme, band of uacaris stopped and rested within 30m of howlers having passed them with apparent indifference. Uacaris made no observable response.	22 mins (full resting time for all visible group members)
Cebus albifrons	17	11	Uacaris in mid-canopy, above the capuchins which were travelling in the understory. Though separated by 4-5 vertical m, their proximity was treated with harsh calls, pilerection and some branch-shaking by adult uacarís. Both groups contained several females with recent young. The *C. albifrons* group did not respond to the aggressive displays.	6 mins.
Cebus albifrons	11, 5, 6, 3,	9, 7, 3, 6	The two species treated each other with apparent mutual indifference. Young present, but more mature.	1 - 5 mins.
Cebus apella	11	15	Two groups came into proximity at terra firme-igapó interface. Uacaris left *Swartzia polyphylla* (Fab.: Pap) trees on whose young leaves they had been feeding and moved into the igapó. *C. apella* replaced them in the trees (whose unrolled leaves were infested with caterpillars).	5 mins.
Cebus apella	6?, 5, 3	8, 11, 8	Two groups travelling within 10m but in opposite directions, uacaris in igapó, capuchins in terra firme. Uacaris made no observable response.	1-4 mins.

Appendix IV-3: Interactions with Other Primates – continued 1				
Primate Species	***No. of Uacaris***	***No. of Individuals of Other Primate Species***	***Type of Interaction***	***Duration***
Saimiri sciureus	15	16	the two were not intermixed, but the *Saimiri* closely followed the uacarís (although slightly lower in the canopy).	17 mins. (then lost)
Saimiri sciureus	12	15	as above	11 mins. (then lost)
Saimiri sciureus	8	6	as above. Splitting was fully complete, with an all-uacari and an all-*Saimiri* group going off at angles. No calls, no obvious event precipitated this.	13 minutes (then groups split)

Appendix IV-4: Behavioural Responses of Uacaris to Non-primate Species

Species Involved	***Interaction Type***	***No. Times Seen***	***Uacari Behavioural Response***
Ara ararauna (Blue-and-yellow Macaw), *A. macao* (Scarlet Macaw: Psittidae)	Macaws (generally calling) flew over canopy in which group was foraging	15	No observable reaction (11). Animals foraging highest in canopy glanced upwards (4).
Amazona farinosa (Mealy Amazon Parrot), *A. festiva* (Festive Amazon Parrot) *Amazona* spp. parrots (Psittidae)	Parrots flew over canopy in which group was foraging	37	No observable reaction (26). Look upward (5). Loop upward, *chock* calls (3). Look upward, *chock* and move down into denser canopy (3: 2 mothers with babies; 1 adolescent).
Amazona festiva, *Amazona* spp.	Parrot, perched, call close to uacari group (within 100m)	7	No observable reaction.
Ramphastos tucanus (White-throated Toucan: Rhamphastidae)	Toucans fly over canopy in which uacari group was foraging	4	Uacaris glanced up (twice). Had no observable reaction (twice).

IV-4: Responses of Uacaris to Non-primates – continued 1

Species Involved	***Interaction Type***	***No. Times Seen***	***Uacari Behavioural Response***
Ramphastos tucanus	Toucan calls close to group (within 100m)	7	No observable reaction.
Ramphastos tucanus and *Ramphastos* sp.	Loose association between group of 20 uacarí was seen moving in loose association with two species of toucan	1	In terra firme. Birds remained feeding in area as, after about 20 minutes, uacaris moved away. Uacaris eating near-ripe seeds of *Bombacopsis macrophylla* (Bombacaceae), and young leaves of *Lecythis pisonis* (Lecythidaceae). Toucans eating ripe fruits of *Miconia poeppingii* (Melastomataceae). Birds and monkey appeared mutually indifferent.
Buteogallus urubitinga (Great Black Hawk, 2), *Busarellus nigricollis* (Black-collared Hawk, 2) *Leocopternis schistacea* (Slate-coloured Hawk, 1) *Spizaetus tyrannus* (Black Hawk-eagle, 1) (Acccipitridae)	Raptor in transit flew over canopy occupied by uacari group	6	On three occasions the monkeys appeared indifferent, possibly because the birds were rather high up (more than 15m above the canopy). On three occasions when in-transit raptors flew lower than this several members of the group looked up and multiple *chock* calls were heard. Animals continued to chock for up to three minutes after the bird had passed and some glancing skywards was still occurring 5 minutes after the passage.
Buteogallus urubitinga, *Busarellus nigricollis* *Spizaetus tyrannus*. (Accipitridae)	Raptor in transit flew over canopy occupied by uacari group	3	On these occasions the raptors displayed an obvious interest in the activity of the uacari group. On one occasion each, a *B. nigricollis* and an *S. tyrannus* flew back-and-forth over the group's location. Group members responded with *chock* and *cheng* calls, and several retreated to low branches in the canopy, others to near the main trunk, and at least three dropped out of the canopy and clung to main trunks in a posture reminiscent of a *Pithecia* about to leap. On both occasions, the calls continued for some 15 minutes after the raptors left (the uacaris staying in the immediate area for this time).

Appendix IV-4: Responses of Uacaris to Non-primates – continued 2

Species Involved	***Interaction Type***	***No. Times Seen***	***Uacari Behavioural Response***
Buteogallus urubitinga, *Busarellus nigricollis*, *Chondroheirax unicinctus (*Hook-billed Kite), *Rostrathamus socialbilis* (Snail Kite) (all Acccipitridae)	Raptor calls close to uacari group	11	Animals oriented to call on 7 occasions, chocked on 5 occasions and moved lower into canopy on two occasions. On one occasion they appeared indifferent.
Cathartes aura (Turkey Vulture), *Coragyps atratus* (Black Vulture) (both Cathartidae)	Vulture flew over group	47	Reaction depended on proximity to group. If 15 or more m above the canopy, the bird was ignored. But, on the few (n=5) instances that one flew close to the canopy it elicited if it flew closer than 10m above the canopy, *chock* calls and movements into the lower canopy occurred (N=4).
Elanoides forficatus (Swallow-tailed Kite: Acccipitridae)	Swallow-tailed Kite flew over uacari group	4	No observable reaction
Micrastur Forest falcon (possibly Slaty-backed, *M. mirandollei*: Falconidae)	Small raptor flew through forest close to uacaris	2	No observable reaction
Egretta spp. (Egrets) and *Ardea* spp. (Herons: all Ardeidae), respectively	Egrets and herons flew close to group	5	No observable reaction
Cairina moschata (Wild Muscovy Duck: Anatidae)	Ducks flew out of roost in tree in front of travelling uacari group	2	No observable reaction, but a couple of mild *chock* calls heard (uacaris normally travel silently)
Mesembrinibis cayennensis (Green Ibis: Threskiornidae)	Ibis flew close to group	3	Once treated with indifference. Twice elicited *chock* calls from adult females. At the time slightly smaller animals (adolescents from previous years?) were foraging for berries in *Eugenia* bushes near water.

Appendix IV-4: Responses of Uacaris to Non-primates – continued 3

Species Involved	***Interaction Type***	***No. Times Seen***	***Uacari Behavioural Response***
Picidae, Cerylidae Colombidae. Pipridae, Trochilidae Thraupidae, Trogloditidae	birds flew through, or very close to, uacari group woodpeckers water kingfishers pigeons manakins hummingbirds tanagers wrens	35	No observable reaction
Gabulidae, Funaridae, Thamnophilidae, Thamnophilidae, Tyrnanidae, Bucconidae, Cuculidae	jacamars, woodcreepers, ant-wrens, ant-shrikes, flycatchers, nunbirds and anis all followed uacaris		No observable reaction. In no case was the association a protracted one. Instead the impression gained was of a temporary association that lasted for as long as the primates were moving through the territory of a particular individual or pair of birds. The birds were never close to, or intermixed with the uacaris, but always at least 5-8m away, even when obviously tracking them through the forest. On four occasions ant-wrens gave alarm calls immediately after uacaris gave *chock* call, making it possible that the birds were travelling with the monkeys more for their predator-detecting capacities than their abilities to beat-up insects. Food collecting rates with and without uacaris are compared in Tables IV-22 and IV-23 for four species of bird seen associated with uacaris.
Tamandua tetradactyla (Large Tree Anteater: Myrecophagidae)	*Anteater within 20m of group*	5	No observable reaction
Eira barbara (Tayra: Mustelidae)	*Tayra within 50m of group*	1	Occasional *chock* calls while on ground, switching to a many *chock* calls, and movement away and to higher canopy when tayra ascended a tree trunk and entered lower canopy (was not hunting uacaris)

Appendix IV-4: Responses of Uacaris to Non-primates – continued 4

Species Involved	***Interaction Type***	***No. Times Seen***	***Uacari Behavioural Response***
Bradypus tridactylus (Pale-throated Sloth: Bradypodidae)	*Sloth within 20m of group*	5	No observable reaction
Panthera onca (Jaguar: Felidae)	*Jaguar calls in distance*	2	On both occasions I was in auditory but not visual contact with the uacaris. One on occasion the jaguar's deep raspy cough-like vocalization elicited a series of *chock* calls that lasted (with diminishing frequency) nearly ten minutes. In the other event, there were fewer chock calls, but, judging from the diminution in the loudness of the twitter calls, the animals moved away quickly.
Iguana iguana (Iguana: Iguanidae)	*Large iguana (≥ 1m) on branch within 1m of uacari group*	3	In each case, two to three *chock* calls, given by adolescents. The group was already moving away, and continued to do so without apparent increase in speed.
Caiman crocodile, Melanosuchus niger (Spectacled Caiman, Black Caiman: both Alligatoridae)	*Large caiman (≥2m) enters water within 10m of feeding uacaris*	2	No observable reaction
Unidentified lizards	*Small lizards on branch*	3	Once, ignored on neighboring branch at eye level (adult). Once, attracted attention when it moved, and uacari (adolescent) moved towards it, losing interest when reptile went into dense epiphytes. Once, to scuttle of escaping lizard uacari (adult) appeared startled, drawing back and uttering three *chocks* in quick succession, before moving on.
Hylidae (possibly *Hyla* or *Osteocephalus* sp.: tree frogs)	*Frogs in canopy*	2	One grabbed leaping from epiphyte thicket, as uacaris passed by. One ignored as sat still on *Philodendron* and uacari foraged nearby.

Appendix IV-4: Responses of Uacaris to Non-primates – continued 5

Species Involved	***Interaction Type***	***No. Times Seen***	***Uacari Behavioural Response***
Probably Arapaima or Arowara (*Arapaima gigas* and *Osteoglossum* sp.: Osteoglissidae, respectively) and/or Tambaqui (*Colossoma macropomum*: Characidae)	*Large fish breaks surface and leaps.*	5	Look towards noise (3). No observable reaction (2)
Unknown trees	*Very large branch falls or tree falls*	11	No observable reaction (5). Look towards noise but continue activities (3: 2 adolescents, 1 female with baby), pause, utter short series of *chocks* (2: 1 adolescent, 1 female with baby), pause with no chocks, no look (1 adult).

Chapter 5: Appendices

Appendix V-1: List of Plant Species Eaten by Cacajao ouakary at Jaú National Park, including Ranked Order of Feeding Records

KEY:

Type: E = epiphyte, Tc = canopy tree, Tu = understory tree, Pc = canopy palm, Pu = understory palm, S = shrub, V = vine

Habitat: I = igapó, Tf = terra firme (inc. borokotò and capoeira)

Part: A = aril, Fb = immature flower (or inflorescence), Fl = mature flowe (or inflorescence), Fs = flower stalk, Fw = whole fruit*, La = leaf base, Lj = leaflet junctions, Lm = mature leaf, Lu = leaf bud, Ly = young leaf, Pb = pseudobulb, Pi = pith, Pu = pulp, Si = immature seed, Sg = seedling, Sm = mature seed, Wd = dead wood.

Period: Phase 1 (Oct-Feb), 2 = Phase 2 (Mar - Jun), 3 = Phase 3 (Jul - Sep).

Notes: **1:** the synconia of *Ficus* spp. were functionally considered to be whole fruit

2: Rank calculated on sum of Feeding Records for all diet items combined. Where numbers tied, . priority in ranking was determined alphabetically by genus name

Species	***Local Name***	***Plant Type***	***Habitat***	***Part Eaten***	***Phase***	***No. Indirect Records (per Phase)***	***No. Direct Obs. (per Phase)***	***Total No. Feeding Records***	***Rank (no. records)***
Annonaceae								**43**	
Annona sp.	Envira	Tu	I	Si	2	23		23	64 (23)
Duguettia sp.	Envira	Tu	I	Fl	3	5		5	104 (5)
Gautteria sp.	Envira	Tu	I	Si	1		10	10	76 (15)
Gautteria sp.	Envira	Tu	I	Fl	2, 3		2,3	5	
Apocynaceae								**268**	
Aspidosperma nitida	Sacos de onça	V	Tf	Si	3	3		3	114 (3)
Malouetia flavescens	Pincel	V	I	Si	1,2	57/113		170	16 (170)
Malouetia sp. 2	Pincel com fenda profunda	V	I	Si	2	79		79	35 (79)
Tabernaemontana sp.	Jarmin-do-igapó	V	I	Fl	3	7		7	100 (7)
Araceae								**4**	
Philodendron cf. *megalophyllum*	Ambé	E	I	Fb	1, 3	1/3		4	112 (4)
Arecacae								**28**	
Astrocaryum jauari	Jauarí	Pc	Tf	Fw	1	8		8	91 (8)
Attalea maripa	Inajá	Pc	Tf	Pu	1,3	5/6		11	83 (11)
Leopoldinia pulchra	Jará	Pu	I	Sg	1	9		9	89 (9)
Bignoniaceae								**26**	
Distictella sp.		Tc	I	Fl	3		2	2	129 (2)
Tabebuia barbata	Rabo de capitarí	Tc	I	Fl	3	21		21	63 (24)
Tabebuia barbata	Rabo de capitarí	Tc	I	Si	3		3	3	
Bombacaceae								**32**	
Bombacopsis macrocalyx	Coração do inambú	Tc	Tf	Si	1	32		32	54 (32)

V-1: Plant Species Eaten by Cacajao ouakary – continued 1

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Boraginaceae								**51**	
Cordia sp. 1	?	Tc	I	Lm	3	1		1	43 (48)
Cordia sp. 1	?	Tc	I	Lu	3	15		15	
Cordia sp. 1	?	Tc	I	Ly	2,3	1/31		32	
Cordia sp. 2	?	Tc	Tf	Ly	1	3		3	118 (3)
Bromeliaceae								**87**	
Aechmea mertensii	Tufo verde *or* Orquidea tufo	E	I	La	1,2,3	22/30/15	10	77	30 (87)
Aechmea mertensii	Tufo verde *or* Orquidea tufo	E	I	Fs	1	10		10	
Burseracae								**4**	
Protium sp.		Tc	Tf	Si	1		4	4	113 (4)
Chrysobalenaceae								**68**	
Couepia paraensis	Uixi de peixe	Tc	I	Pu	2	21		21	68 (21)
Licania c.f. *apetala*	?	Tc	Tf	Si	1		6	6	99 (6)
Licania heteromorpha	Moela de mutum	Tc	I	Si	1	28		28	47 (41)
Licania heteromorpha	Moela de mutum	Tc	I	Pu	2	11	2	13	
Clusiaceae								**24**	
Calophyllum brasiliense	Jacareubá	Tc	I	Si	2	8		8	92 (8)
Clusia c.f. *leprantha*	Apuí	E	I	Pi	3		4	4	109 (4)
Clusia sp.	Apuí	E	I	Fb	3	2		2	128 (2)
Lorostemon sp.	Pauxubarana	Tu	I	Si	2	10		10	87 (10)
Combretaceae								**826**	
Buchenavia ochrograma	Periquitera *or* Tanimbucá	Tc	I	Si	1,2	23/392	80/119	614	3 (742)
Buchenavia ochrograma	Periquitera *or* Tanimbucá	Tc	I	Lu	3		17	17	
Buchenavia ochrograma	Periquitera *or* Tanimbucá	Tc	I	Ly	3	40	71	111	
Buchenavia sp.	Pau-de-Vidreo	Tc	I	Ly	1,3	37/7	21/19	84	32 (84)

Appendix V-1: Plant Species Eaten by Cacajao ouakary – continued 2

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Convolvulaceae									
Maripa sp.	?	V	Tf	Si	1	6		6	101 (6)
Cyperaceae								**5**	
Scleria tenacissima	Tiririca	V	I	Lb	1, 3	4,/1		5	106 (5)
Ebenaceae								**80**	
Diospyros cavalcantei	Presente do Thais	Tu	I	Si	1,2	27/17	4/3	51	40 (51)
Diospyros kondan	?	Tu	I	Si	2	21		21	69 (21)
Diospyros manaunsis	Envia	Tc	I	Si	2	8		8	94 (8)
Elaeocarpaceae								**16**	
Sloanea sp.	?	Tc	I	A	2		7	7	75 (16)
Sloanea sp.	?	Tc	I	Si	2		9	9	
Euphorbiaceae							**793**		
Amanoa longifolia	Taquarí	Tc	I	Si	2	16	154	170	13 (200)
Amanoa longifolia	Taquarí	Tc	I	Ly	3	26	4	30	
Concerveiba sp.	?	Tu	I	Si	2	3		3	117 (3)
Croton sp.	?	Tu	I	Si	2	3		3	119 (3)
Discocarpus cf. *spruceanus*	?	Tc	I	Si	2,3	16,7		23	65 (23)
Hevea spruceana	Seringa	Tc	I	Lj	1	24		24	22 (140)
Hevea spruceana	Seringa	Tc	I	Si	1, 2	38/9	/14	61	
Hevea spruceana	Seringa	Tc	I	Pi	1,2, 3	4/ 2 / 22	5/2/19	54	
Hevea sp.	Seringa torrada	Tu	I	Si	2	1	2	3	122 (3)
Mabea nitida	Seringaí	Tc	I	Si	1, 2	150/159	19/19	347	6 (397)
Mabea nitida	Seringaí	Tc	I	Fl	2,3	8/24		32	
Mabea nitida	Seringaí	Tc	I	Ly	3	37	18	55	
Maprounea guianensis	Coraçaozinho	Tc	I	Si	2,3	1/23		24	61 (24)
Fabaceae: Caesalpinoidae							**168**		
Acacia sp.	Cipó sorrisa verde	V	I	Si	2	81		81	33 (81)
Acosmium nitens	Itaubarana	Tc	I	Ly	3	28		28	57 (28)
Cynometra bauhiniifolia	Alvo de caba	Tu	I	Si	2	18		18	70 (18)
Sclerolobium hypoleuca	Taxi do igapó	Tc	I	Si	1,2	17/19		36	52 (36)
Sclerolobium sp. 2	Taxi do terra firme	Tc	Tf	Si	1	5		5	107 (5)

Appendix V-1: Plant Species Eaten by Cacajao ouakary – continued 3

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Fabaceae: Mimosoidae							**543**		
Hydrochorea marginata	Pulero de pato	Tc	I	Fw	1	1	3	4	7 (285)
Hydrochorea marginata	Pulero de pato	Tc	I	Fl	2,3	7/32		39	
Hydrochorea marginata	Pulero de pato	Tc	I	A	2	9		9	
Hydrochorea marginata	Pulero de pato	Tc	I	Ly	1,3	69,152		221	
Hydrochorea marginata	Pulero de pato	Tc	I	Si	2,3	1/11		12	
Inga obidensis	Ingaxixica	Tu	Tf	A	1	45	4	49	42 (49)
Inga rhynchocalyx	Ingaxixica	Tu	Tf	A	1	6	4	10	86 (10)
Macrolobium acacifolium	Arapurí	Tc	I	Si	2	76	3	79	17 (168)
Macrolobium acacifolium	Arapurí	Tc	I	Ly	1, 3	35, 52		87	
Macrolobium multijugum	Arapurí redondo	Tc	I	Si	2	16		16	74 (16)
Parkia discolor	Arapari	Tc	I	Si	2	8	7	15	77 (15)
Fabaceae: Papilionoidae								**868**	
Aldinia heterophylla/latifolia	Macucu	Tc	I	Si	1,2,3	9/35/31	5/ /24	104	25 (104)
Clitoria javitensis	Cipó sem vergonha	V	I	Fl	3	14		14	79 (14)
Dalbergia inundata	Cipó Tucunaré	V	I	Ly	3	27		27	58 (27)
Ormosia sp.	Tento	Tc	I	Ly	2,3	12/103	5/10	130	19 (155)
Ormosia sp.	Tento	Tc	I	Si	2	8		8	
Ormosia sp.	Tento	Tc	I	Pi	3		17	17	
Swartzia laevicarpa	Sabuarana	Tc	I	A	2,3		40/38	78	36 (78)
Swartzia cf. *oblancifolia*	?	Tc	Tf	Si	1	4		4	114 (4)
Swartzia acuminata	Arabá	Tc	I	Fw	1,2	62/57	25/3	147	5 (484)
Swartzia acuminata	Arabá	Tc	I	Si	2	87	8	95	
Swartzia acuminata	Arabá	Tc	I	A	2	100	11	111	
Swartzia acuminata	Arabá	Tc	I	Ly	3	84	43	127	
Swartzia sp.	Arabá gorda	Tu	I	Si	2	2		2	133 (2)

Appendix V-1: Plant Species Eaten by Cacajao ouakary – continued 4

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Flacourtiaceae								**45**	
Casearia sp.	Uva de macaco	Tu	I	Fw	2,3	20/	/12	32	55 (32)
Laetia corymbulosa	Tauri do Tambaqui	Tu	I	Fw	3		13	13	81 (13)
Gesneriaceae								**63**	
Codonanthe crassifolia	Cipó de formiga	V	I	Fl	1,2,3	24 / /13	3/7/2	49	37 (63)
Codonante crassifolia	Cipó de formiga	V	I	Lm	1	18		18	
Hippocrataceae								**114**	
Salacea sp. 1	Buxexa de velho do terra firme	Tu	Tf	Si	1	6	9	15	78 (15)
Salacea sp. 2	Buxexa de velho do igapó	Tc	I	Si	2	11		11	84 (11)
Tontalea sp.	Cipó pitomba	V	I	Pu	3	54	34	88	29 (88)
Humiriacae								**35**	
Humiriastrum cuspidatum	Tucano patuá 2	Tu	I	Pu	2	13		13	80 (13)
Schistostemon macrophyllum	Tucano patuá	Tc	I	Pu	2	22		22	66 (22)
Lauraceae								**8**	
Endlicheria chalisa	Louro Abacatira na	Tc	I	Fl	3	4		4	95 (8)
Endlicheria chalisa	Louro Abacatira na	Tc	I	Pi	3	4		4	
Lecythidaceae								**1986**	
Cariniana cf. *micrantha*	Xaru	Tc	Tf	Si	1		7	7	96 (7)
Couratari cf. *stellata*	Xaru	Tc	Tf	Si	1		5	5	103 (5)
Couratari c.f. *tenuicarpa*	?	Tc	I	Fl	3	187		187	15 (187)
Eschweilera c.f. *romeu-cardosoi* or *E. wachenheimii*	Xaruzinho	Tu	Tf	Si	1	43		43	49 (43)
Eschweilera corrugata	Xaru	Tc	Tf	Si	1	3		3	120 (3)
Eschweilera parviflora	Mata-mata	Tc	Tf	Si	1	3	3	6	98 (6)

Appendix V-1: Plant Species Eaten by Cacajao ouakary – continued 5

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Eschweilera tenuifolia	Macacaca-ricuia	Tc	I	Fl	1,2	175/163	50/46	434	2 (1676)
Eschweilera tenuifolia	Macacaca-ricuia	Tc	I	Si	1, 2	73/642	48/285	1048	
Eschweilera tenuifolia	Macacaca-ricuia	Tc	I	Ly	3	17	19	36	
Eschweilera tenuifolia	Macacaca-ricuia	Tc	I	Sg	1	145	23	168	
Eschweilera sp. 2	Xurú	Tc	I	Si	2	1		1	135 (1)
Lecythis pisonis	Sapucaia	Tc	Tf	Ly	1	24	31	55	60 (55)
Lecythis rorida	Tauari *or* xurú	Tu	Tf	Si	1	3		3	123 (3)
Maphigiaceae								**129**	
Brysonima puntulata	Jacaré café	Tc	I	Si	2	86		86	31 (86)
Burdachia prismatocarpa	Pau de Vidreo	Tc	I	Si	2	43		43	48 (43)
Melastomataceae								**41**	
Bellucia cf. *grossularoides*	Goiaba de Anta	Tu	Tf	Si	1	3		3	116 (3)
Tocoa sp.	Tintarana	Tc	Tf	Fw	1	18	20	38	51 (38)
Memcylaceae								**43**	
Mouriri guianensis	Araça sem pé	Tu	I	Si	3	20	23	43	50 (43)
Moraceae								**14**	
Ficus sp. 1	?	Tu	Tf	Lm	1,2	3/1		4	85 (10)
Ficus sp. 1	?	Tu	Tf	Ly	1	6		6	
Tromphis sp.	Tanimbuca do igapó	Tc	I	Si	2	4		4	126 (4)
Myristicaceae								**12**	
Iryanthera guianense	Ucuuba-puná	Tc	Tf	Si	1		7	7	97 (7)
Osteophyllum platyspermum	?	V	Tf	Si	1	2		2	131 (2)
Virola cf. *surinamensis*	Ucuuba	Tc	Tf	Si	1	3		3	127 (3)
Myrtaceae								**952**	
Calytranthes cf. *creba*	Araçá escorrega macaco	Tu	I	Si	2	151	9	160	18 (160)
Calyptranthes sp. 1	Araçá	Tu	I	Fl	1	10	11	21	67 (21)
Eugenia gomesiana	Araçá	B	I	Si	2	179	23	202	12 (202)
Eugenia sp. 1	Araçá boi	Tu	I	Si	2	45	8	53	38 (53)

Appendix V-1: Plant Species Eaten by Cacajao ouakary – continued 6

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Eugenia sp. 2	Araçá verde grande	B	I	Si	2	17	17	34	53 (34)
Eugenia sp. 3	Araçá verde	B	I	Si	2	18	26	44	46 (44)
Myrcia cf. *grandis*	Araçá vermelhao	Tu	I	Pu	3	23	6	29	56 (29)
Myrcia sp. 1	Araçá vermelho	Tu	I	Si	2	25	2	27	59 (27)
Marlierea umbraticola	Araça branca	B	I	Si	2	44	7	51	26 (102)
Marlierea umbraticola	Araça branca	B	I	Fw	2	44	7	51	
Olacaceae								**280**	
Chaunochiron loranthoides	Chapau-zinho	Tc	I	Si	2	269	8	277	9 (277)
Heisteria sp.	Mamadeira de anta	Tu	I	Si	3	3		3	121 (3)
Orchidaceae								**2**	
Trigonium sp. ?	Orquidea	E	I	La	2	1		1	134 (2)
Trigonium sp. ?	Orquidea	E	I	Pb	3	1		1	
Passifloraceae								**32**	
Passiflora costata	Maracujá de mata	V	I	Fl	3	6		6	102 (6)
Passiflora phellos	Maracujá de mata	V	I	Fl	3	18		18	71 (18)
Passiflora sp. 1	Maracujá de mata	V	I	Si	2	2		2	110 (4)
Passiflora sp. 2	Maracujá de mata	V	Tf	Si	1	2		2	111 (4)
Passiflora sp. 1	Maracujá de mata	V	I	Pu	2	2		2	
Passiflora sp. 2	Maracujá de mata	V	Tf	Pu	1	2		2	
Piperacae								**2**	
Piper sp.	Cacete do gringo	B	I	Fl	3	2		2	132 (2)
Polygalaceae								**124**	
Securidaca sp.	Cresto de Galo	V	I	Si	2	121	3	124	23 (124)
Proteaceae								**50**	
Panopsis rubescens	?	Tu	I	Si	1	50		50	41 (50)

Appendix V-1: Plant Species Eaten by Cacajao ouakary – continued 7

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Quiinaceae								**13**	
Quinea negrensis	Uva de macaco listrada	Tu	I	Fw	2	5	3	8	83 (13)
Quinea negrensis	Uva de macaco listrada	Tu	I	Si	2	2	3	5	
Rubiaceae								**239**	
Duroia aquatica	Cunhum liso	Tc	I	Si	1,2	7/6	2/2	17	73 (17)
Duroia gransabanensis	Cunhum da anta	Tu	Tf	Si	1	2		2	130 (2)
Duroia velutina.	Cunhum	Tc	I	Pu	1,2	4/41	5/6	56	11 (220)
Duroia velutina.	Cunhum	Tc	I	Si	1,2	4/139	5/16	164	
Sapindaceae								**3**	
Paullinia rufescens	Bala branca	V	I	Si	1		3	3	124 (3)
Sapotaceae								**3829**	
Chromolucuma rubiflora	Abiurana	Tc	I	Si	2	254	23	277	10 (227)
Chrysophyllum argentum aurateum	Abiurana ferro	Tc	Tf	Si	1	7	1	8	93 (8)
Chrysophyllum sparsifolium	Abiurana ferro	Tc	Tf	Si	1	7	2	9	88 (9)
Chrysophyllum sanguinolentum balata	Balata brava	Tc	Tf	Si	1		4	4	108 (4)
Chrysophyllum s. sanguinolentum	Balata mansa	Tc	Tf	Si	1	48	4	52	39 (52)
Eleoloma glabrescens	Caramuri	Tc	I	Si	1,2	26/109	10/7	152	20 (152)
Manilkara b. bidentata	Macaran-duba	Tc	I	Si	2	104	9	113	24 (113)
Micropholis venusta	Bicó de Japó	Tc	I	Si	1,2	172/1582	4/30	1718	1 (1788)
Micropholis venusta	Bicó de Japó	Tc	I	Ly	2	4	1	5	
Micropholis sp.	?	Tc	I	Si	2	46		46	45 (46)
Pouteria caimito	Abiurana redondo	Tc	I	Si	2		9	9	90 (9)
Pouteria cuspidata	Abiuarana	Tc	I	Si	2	95		95	28 (95)
Pouteria elegans	Cabeçudo	Tc	I	Fw	1	11	7	18	4 (565)
Pouteria elegans	Cabeçudo	Tc	I	Sg	1	6		6	
Pouteria elegans	Cabeçudo	Tc	I	Si	1,2	58/413	25/21	517	

Appendix V-1: Plant Species Eaten by Cacajao ouakary – continued 8

Species	*Local Name*	*Plant Type*	*Habitat*	*Part Eaten*	*Phase*	*No. Indirect Records (per Phase)*	*No. Direct Obs. (per Phase)*	*Total No. Feeding Records*	*Rank*
Pouteria elegans	Cabeçudo	Tc	I	Ly	3	7	3	10	
Pouteria elegans	Cabeçudo	Tc	I	Pi	3		8	8	
Pouteria gomphifolia	Abiuarana	Tc	Tf	Si	1	261	17	278	8 (278)
Pouteria cf. *procera*	Abiurana bico	Tc	I	Si	1,2	7/63	3/6	79	34 (79)
Pouteria tarumaensis	Caramurí do igapó	Tc	I	Si	2	44	4	48	44 (48)
Pouteria ucuqui	Uiqui	Tc	Tf	Si	1		3	3	125 (3)
Pouteria 'cabeçudo' 1	Cabeçudo	Tc	I	Sg	1	3	5	8	72 (18)
Pouteria 'cabeçudo' 1	Cabeçudo	Tc	I	Si	2		3	3	
Pouteria 'cabeçudo' 1	Cabeçudo	Tc	I	Ly	3		7	7	
Pouteria 'cabeçudo' 2	Cabeçudo elongado	Tc	I	Si	2	119	71	190	14 (190)
Pouteria 'cabeçudo' 3	Cabeçudo redond-inho	Tc	I	Si	2	87	9	96	27 (96)
Simaroubaceae								**147**	
Simaba orinocensis	Cajurana	Tu, V	I	Si	2	147		147	21 (147)
Siparunaceae								**1**	
Siparuna sp.	?	Tu	Tf	Si	3	1		1	136 (1)
Theaceae								**21**	
Ternstroemia candolleana	?	Tu	I	Si	2, 3	/10	11/	21	70 (21)
Viscacae								**5**	
Phoradendron poeppigii	Parasita	E	I	Fb	2	5		5	105 (5)
Unidentified								**92**	
Tree species 1		T	I	Lm	3	10		10	
Tree species 2		T	I	Lm	3	10		10	
Tree species 3		T	I	Lm	3	10		10	
Tree species 4		T	I	Lm	3	10		10	
Tree species 5		T	I	Ly	3	10		10	
Tree species 6		T	I	Ly	3	10		10	
Tree species 7		T	I	Ly	3	10		10	
Tree species 8		T	I	Lu	3	10		10	
Tree species 9		T	I	Fb	3	10		10	
Tree species 10	Bouriri	T	I	Si	2	1		1	
Tree species 11		T	I	Fl	2	1		1	

Appendix V-2 Plant Species with Multiple Parts Eaten by Cacajao ouakary

***Key**: A = aril, Fl = mature flower (or inflorescence), Fs = flower stalk, Fw = whole fruit, La = leaf base, Lj = leaflet junctions, Lm = mature leaf, Lu = leaf bud, Ly = young leaf, Pi = pith, Pu = pulp, Si = immature seed, Sg = seedling*

Species	***A***	***Fl***	***Fs***	***Fw***	***La***	***Lj***	***Lm***	***Lu***	***Ly***	***Pi***	***Pu***	***Si***	***Sg***
Aechmea mertensii			*x*		*x*								
Amanoa oblongifolia									*x*			*x*	
Buchenavia ochrogramma								*x*	*x*			*x*	
Codonanthe crassifolia		*x*					*x*						
Duroia velutina											*x*	*x*	
Eschweilera tenuifolia		*x*							*x*			*x*	*x*
Hevea spruceana						*x*				*x*		*x*	
Hydrochorea marginata	*x*	*x*		*x*					*x*			*x*	
Licania heteromorpha											*x*	*x*	
Mabea nitida		*x*							*x*			*x*	
Macrolobium acaciifolium									*x*			*x*	
Marlierea umbraticola											*x*	*x*	
Micropholis venusta									*x*			*x*	
Ormosia sp.										*x*		*x*	
Pouteria 'cabeçudo' 1									*x*			*x*	*x*
Pouteria elegans				*x*					*x*	*x*		*x*	*x*
Quiinea negrensis				*x*								*x*	
Sloanea sp.	*x*											*x*	
Swartzia acuminata	*x*			*x*					*x*			*x*	
Tabebuia barabata		*x*										*x*	

***Appendix V-3: Non-plant Foods in the Diet of* Cacajao ouakary**

Species	***Type***	***No. Records***	***Habitat***	***Phase***
Ants	adult	11	Ig	2 (5), 3 (6)
Ants	Larvæ, adults	3	Ig	3 (3)
Coleoptera	larvæ	9	Ig	3 (9)
Lepidoptera	adults			
Lepidoptera	larvæ (free)	7	Ig	2(6) 3(1)
Caterpillars (fam.:	From young leaves of *Swartzia acuminata*	84	Ig	3(84)
Fulgorida	Adults and nymphs	(1)	Ig	3 [1]
Orthoptera	Adult	8	Ig	2 (3), 3 (6)
Ephemeroptera	Adult	23	Ig	1 (7), 2 (16)
Araiidae	Adult	10	Ig	2 (5), 3 (5)
Isoptera	Adult	9	Ig	2 (3), 3 (6)
Isoptera	Alate	11	Ig	2 (11)
Polybela sp.	Nest with adults and larvæ	9	Ig	1(2), 2(3), 3(4)
Orthoptera	imago	8	Ig	2(2) 3(6)
Unidentified Larvæ	From new stems of *Ocotea* sp.	6	Ig	3(6)
Stem borers	In new stems of Annonaceae	4	Ig	1(1) 3(3)
Stem borers	New stems of *Pouteria elegans*	27	Ig	1(27)
Stem borers	Abourana	3	Ig	1(3)
Stem borer	New stems of *Hydrochorea marginata*	10	Ig	1(10)
Scarabid beetle larvæ	Dead Taxi wood	3	Ig	1(3)
Stem borers	*Pouteria elegans* leaf petioles	7	Ig	1(7)

Appendix V-3: Non-plant Foods in C. ouakary Diet – continued 1

Species	*Type*	*No. Records*	*Habitat*	*Phase*
Catterpillars	In folded leaves of *Lecythis pisonis*	24	Ig	1(24)
Insect larvæ	Dead leaves	6	Ig	2(2) 3(4)
Insect larvæ	In leaf petioles of *Clusia* sp.	7	Ig	1(7)
Unidentified on branch	Taken from arm resting on branch – impossible to tell what eaten or how many (7 = minimum observed)	(1)	Ig	1(7)

Appendix V-4: Number of Species Eaten per Diet Category in each Phase and Habitat.

Key: A = aril, Fb = immature flower (or inflorescence), Fl = mature flower (or inf.), Fs = flower stalk, Fu= fungus Fw = whole fruit*, La = leaf base, Lj = leaflet junctions, Lm = mature leaf, Lu = leaf bud, Ly = young leaf, Pb = pseudobulb, Pi = pith, Pu = pulp, Si = immature seed, Sg= seedling, Sm = mature seed, Wd = dead wood, * including fig synconia

Habitat & Phase	***Ar***	***Fb***	***Fl***	***Fs***	***Fu***	***Fw***	***La***	***Lb***	***Lj***	***Lm***	***Lu***	***Ly***
Phase 1 - Ig	0	1	3	1	1	3	1	1	1	1	0	2
Phase 1 - Tf	0	0	0	0	0	2	2	0	0	3	0	3
Phase 2 - Ig	4	1	4	0	0	3	1	0	0	0	0	4
Phase 2 - Tf	0	0	0	0	0	0	1	0	0	0	0	0
Phase 3 - Ig	1	3	9	0	0	2	1	1	0	4	15	17
Phase 3 - Tf					0							

Habitat & Phase	***Pb***	***Pi***	***Pu***	***Si***	***Sg***	***Sm***	***Wd***	***Total Plant Sp.***	***Total Animal Sp.***	***Total Species***	***Niche Breadth Index***
Phase 1 - Ig	0	1	1	20	4	0	0	41	10	51	0.895
Phase 1 - Tf	1	0	2	25	0	0	0	38	2	40	0.5851
Phase 2 - Ig	0	4	4	58	0	0	0	79	12	91	0.568
Phase 2 - Tf	0	0	0	0	0	0	0	1	0	1	1
Phase 3 - Ig	0	5	2	7	0	2	1	67	13	80	0.5109
Phase 3 - Tf	0	0	1	2	0	0	0	3	0	3	0.943

Appendix V-5: Plant Species Eaten by Cacajao ouakary, *Calculations for Ivlev Selection Ratios (species present in quadrats and with 10 or more feeding records only)*

KEY:
Habitat: I = igapó, Tf = terra firme (inc. borokotò and capoeira)
Part: A = aril, Fb = immature flower (or inflorescence), Fl = mature flower (or inflorescence), Fs = flower stalk, Fw = whole fruit*, La = leaf base, Lj = leaflet junctions, Lm = mature leaf, Lu = leaf bud, Ly = young leaf, Pb = pseudobulb, Pi = pith, Pu = pulp, Si = immature seed, Sg = seedling, Sm = mature seed, Wd = dead wood.
Period: Phase 1 (Oct-Feb), 2 = Phase 2 (Mar-Jun), 3 = Phase 3 (Jul-Sep).
Note: No. records includes records from all three FR sources combined. xxx = no records from quadrats

Rank	*Species*	*Family*	*# Plants in quadrat*	*No. fruit Records*	*Habitat*
1	*Micropholis venulosa*	**Sapo**	**41**	**1738**	**I**
2	*Eschweilera tenuifolia*	**Lecy**	**137**	**1216**	**I**
3	*Buchenavia ochrograma*	**Comb**	**94**	**614**	**I**
4	*Pouteria elegans*	**Sapo**	**146**	**497**	**I**
5	*Swartzia acuminata*	**Fab:Pap**	**6**	**353**	**I**
6	*Mabea nitida*	**Euph**	**75**	**347**	**I**
7	*Hydrochorea marginata*	**Fab:Mim**	**59**	**16**	**I**
8	*Pouteria gomphifolia*	**Sapo**	**7**	**541**	**I**
9	*Chaunochiron loranthoides*	**Olac**	**xxx**	**277**	**I**
10	*Chromolumuma rubiflora*	**Sapo**	**xxx**	**277**	**I**
11	*Duroia velutina*	**Rubi**	**26**	**220**	**I**
12	*Eugenia gomesiana.*	**Myrt**	**2**	**202**	**I**
13	*Amanoa longifolia*	**Euph**	**150**	**170**	**I**
14	*Pouteria 'cabeçudo'* 2	**Sapo**	**8**	**190**	**I**
15	*Couratari* c.f. *tenuicarpa*	**Lecy**	**xxx**	**187**	**I**
16	*Malouetia flavescens*	**Apoc**	**7**	**170**	**I**
17	*Macrolobium acacifolium*	**Fab:Caes**	**17**	**169**	**I**
18	*Eleoloma glabrescens*	**Sapo**	**92**	**152**	**I**
19	*Calyptranthes* cf. *creba*	**Myrt**	**xxx**	**151**	**I**
20	*Simaba orinocensis*	**Sima**	**2**	**147**	**I**
21	*Ormosia* sp.	**Fab:Pap**	**14**	**8**	**I**
22	*Securidaca* sp.	**Poly**	**xxx**	**121**	**I**
23	*Hevea spruceana*	**Euph**	**15**	**52**	**I**
24	*Manilkara b. bidentata*	**Sapo**	**xxx**	**115**	**I**
25	*Aldinia heterophylla/latifolia*	**Fab:Pap**	**5**	**104**	**I**
26	*Ormosia* sp.	**Fab:Pap**	**xxx**	**103**	**I**
27	*Pouteria 'cabeçudo'* 3	**Sapo**	**8**	**96**	**I**
28	*Pouteria cuspidata*	**Sapo**	**xxx**	**95**	**I**
29	*Tontalea* sp.	**Hippo**	**xxx**	**88**	**I**
30	*Buchenavia* sp. 2	**Comb**	**2**	**0**	**I**
31	*Acacia* sp.	**Fab:Caes**	**xxx**	**81**	**I**
32	*Pouteria* cf. *procera*	**Sipo**	**xxx**	**79**	**I**
33	*Malouetia* sp. 2	**Apoc**	**xxx**	**79**	**I**

Appendix V-5: Calculations for Ivlev Selection Ratios – continued 1

Rank	*Species*	*Family*	*# Plants in quadrat*	*No. fruit Records*	*Habitat*
34	*Swartzia laevicarpa*	**Fab:Pap**	**2**	**78**	**I**
35	*Aechmea tessmanni*	**Brom**	**n/a**	**77**	**I**
37	*Codonanthe crassifolia*	**Gesn**	**n/a**	**63**	**I**
38	*Inga obidensis*	**Fab:Mim**	**3**	**59**	**Tf**
39	*Eugenia* sp. 1	**Myrt**	**26**	**53**	**I**
40	*Chrysophyllum s. sanguinolentum*	**Sapo**	**5**	**52**	**Tf**
41	*Brysonima puntulata*	**Malph**		**86**	
42	*Diospyros cavalcantei*	**Eben**	**19**	**51**	**I**
43	*Marlierea umbraticola*	**Myrt**	**xxx**	**102**	**I**
44	*Panopsis rubescens*	**Prot**	**xxx**	**50**	**I**
45					
46	*Cordia* sp. 1	**Bora**	**6**	**0**	**I**
47	*Pouteria tarumaensis*	**Sapo**	**xxx**	**48**	**I**
48	*Micropholis* sp. 2	**Sipo**	**xxx**	**46**	**I**
49	*Burdachia prismatocarpa*	**Malph**	**31**	**43**	**I**
50	*Eugenia* sp. 3	**Myrt**	**3**	**44**	**I**
51	*Corythrophora* sp. (Eschweilera wachenheimi)	**Lecy**	**7**	**43**	**Tf**
52	*Mouriri guianensis*	**Memc**	**7**	**43**	**I**
53	*Tocoa* sp.	**Mela**	**xxx**	**38**	**I**
54	*Sclerolobium hypoleuca*	**Fab:Caes**	**41**	**36**	**I**
55	*Brysonima puntulata*	**Malp**	**xxx**	**86**	**I**
56	*Eugenia* sp. 2	**Myrt**	**3**	**34**	**I**
57	*Bombacopsis macrocalyx*	**Bomb**	**xxx**	**32**	**I**
58	*Casearia* sp.	**Flac**	**3**	**32**	**I**
59	*Myrcia* cf. *grandis*	**Myrt**	**31**	**29**	**I**
60	*Acosmium nitens*	**Fab:Caes**	**13**	**0**	**I**
61	*Licania heteromorpha*	**Chry**	**31**	**41**	**I**
62	*Dalbergia inundata*	**Fab:Pap**	**14**	**27**	**I**
63	*Myrcia* sp. 1 (cf. *paivae*)	**Myrt**	**18**	**27**	**I**
64	*Tabebuia barbata*	**Bign**	**4**	**24**	**I**
65	*Lecythis pisonis*	**Lecy**	**1**	**0**	**Tf**
66	*Maprounea guianensis*	**Euph**	**26**	**24**	**I**
67	*Annona* sp.	**Anno**	**xxx**	**23**	**I**
68	*Discocarpus* cf. *spruceanus*	**Euph**	**13**	**23**	**I**
69	*Schistostemon macrophyllum*	**Humi**	**xxx**	**22**	**I**
70	*Calyptranthes* sp.	**Myrt**	**xxx**	**21**	**I**
71	*Couepia paraensis*	**Chry**	**6**	**21**	**I**
72	*Diospyros kondan*	**Eben**	**1**	**21**	**I**
73	*Ternstroemia candolleana*	**Thea**	**26**	**21**	**I**

Appendix V-6: Diet Species from which Insect-infested Fruits were Recorded

***Amanoa oblongifolia, Bombacopsis macrocalyx, Callophyllum brasiliense, Calyptranthes* cf. *creba, Chaunochiton loranthoides, Diospyros cavalcanteii, Duguettia* sp., *Duroia aquatica, Duroia velutina, Elaeoluma glabrescens, Eschweilera tenuifolia, Eugenia* sp., *Inga obidensis, Inga rhynchocalyx, Licania heteromorpha, Mabea nitida, Macrolobium acaciifolium, Mouriri* sp., *Myrcia* sp., *Parkia discolor, Protium* sp., *Pouteria elegans, Pouteria* sp., *Sloanea* sp., *Swartzia acuminata*.**

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